THE INHERITANCE OF SALT TOLERANCE IN BARLEY (HORDEUM VULGARE L.)

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ABSTRACT

THE INHERITANCE OF SALT TOLERANCE IN

BARLEY (*HORDEUM VULGARE* L.)

by

Abubaker M. Maddur

The differential responses of barley varieties (*Hordeum vulgare* L.) to salt stress in various growth stages suggest that one of the most promising methods to overcome the problem of salt injury to plants is the use of tolerant varieties through a viable breeding program perhaps in the combination with land reclamation and desalination of salty water.

The first step in this direction requires the development of a method to classify large numbers of individual plant genotypes for salt tolerance in various growth stages along with a knowledge of the inheritance of salt tolerance.

A method was developed to screen barley populations for salt tolerance in the germination stage.

Thirty-three varieties were included in the screening test. On the basis of the screening results, six parental varieties were chosen for a diallel cross set in order to investigate the genetic basis of salt tolerance.

The F_2 from the 6 x 6 diallel-cross were tested for salt tolerance in two growth stages; the germination stage and the early growth stage, following germination and early seedling. The data were analyzed according to the Jinks-Hayman diallel-cross analysis.

Salt tolerance in barley appears to be controlled by dominant genes. Dominance seems to be partial in the germination stage and nearly complete in the early growth stage. Non-allelic gene interaction was found to be important in determining salt tolerance in the early growth stage.

Transgressive segregation was observed in some crosses suggesting the possibility of identifying superior crosses.

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by

Abubaker Murtada Maddur

A DISSERTATION

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To my people.....

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (cont'd.)

INTRODUCTION

Soil salinity is a major factor in determining the capacity of the land for agricultural use in the arid zones of the world where rainfall is scarce and seasonal and the underground waters, when found, are often too saline to be of use. Soil salinity becomes important in agriculture when the concentrations of soluble salts in the soil solution reach levels that adversely affect plant growth and yield.

These conditions are by no means restricted to arid climates. For instance, excessive use of fertilizers in intensively farmed lands, or irrigation with saline waters, or with insufficient water or under conditions of poor drainage may also bring about the accumulation of soluble salts to the point where their concentrations seriously impairs productivity. The adverse effects on plant growth of excessive concentration of soluble salts in the root medium are varied. They range from simply inhibiting the growth of some plants and reducing yield, to actually injuring or killing the plant tissues.

The urgent demand to resolve the current world problems of hunger and food shortages, complicated by the rising world population, increases the need to search for means of exploiting the vast areas of saline desert lands and the need for future use of brackish and saline waters for crop irrigation. These challenges can be met by developing salt tolerant plants through a viable breeding program. This should be coupled with plans for the reclamation of desert lands and the desalination of sea water.

The fact that plant species are not equally affected by salinity and the significant variation in salt tolerance encountered in varieties of some species, suggests that plant tolerance to salt stress is under gene control.

The relative high salt tolerance of the barley plant, and the striking performance of some varieties, makes barley a prime candidate among all cereals for any breeding program for salt tolerance. However, adequate information on the subject of the inheritance of salt tolerance is a prerequisite to enable a program of this kind to materialize. This study is designed to

investigate the genetic basis of salt tolerance in the barley plant (*Hordeum vulgare* L.).

REVIEW OF LITERATURE

A "Saline Soil" is one which contains sufficient soluble salts to affect adversely the growth of plants (27).

The surface inch of soil is often more saline than the soil below it. This is a result of evaporation and capillary movement of saline water to the surface. Furrow-irrigated ridges or raised beds (10, 44) enhance this condition.

The cations, calcium, sodium and magnesium, and the anions, chloride, sulfate, bicarbonate and carbonate were generally predominant (12). But most of the salt stresses in nature are due to sodium salts, particularly sodium chloride (32). Symptoms of salt-injured plants are often recognized as stunted growth and smaller darker green leaves (12); also as necrosis or marginal burn (41), and in severe cases final death of the plant (32).

The effects on plant growth of the excessive salt concentrations in the root zone may be mediated by osmotic

effects, or by specific ion effects, or both (12, 27, 32).

The osmotic theory assumes equivalent effects on the growth processes of the plant by such ions as sodium, calcium and of chloride and sulphate (12). This suggests that salt injury to plants was due primarily to physiological scarcity of water, resulting from increased osmotic pressure of the soil solutions (4, 9, 20, 29). The theory's advocates base their ideas on the fact that some symptoms exhibited by salt-injured plants, such as stunted growth and smaller, darker green leaves, closely resembled those symptoms caused by drought stress (20, 29).

The specific ion effect theory, on the other hand, requires the deleterious effects of salts be dependent, necessarily, on the different salts. Salts may exert adverse effects interfering with the plant metabolism by inducing shifts in mineral nutrient status or by causing direct toxicity (12).

The stress actions of similar concentrations of various salts on wheat germination have been reported to decrease, in the order of magnesium, potassium, and sodium (26, 46). Sodium chloride solutions were more depressive

to wheat germination than isosmotic dilutions of sea water and of glucose solutions (12). Similarly, sodium chloride exceeded mannitol in decreasing alfalfa germination, when equivalent isosmotic solutions were compared (41, 43). Excessive absorption of magnesium by plants decreased the absorption of calcium and potassium (12), while sulphate ion enhanced the uptake of sodium at the expense of calcium ions (29). Chloride absorption induced nitrate deficiency in wheat (17).

There is evidence of direct toxicity to various plant species by such ions as sodium (8), chloride (16), boron (21), bicarbonate (15, 23, 39) and phosphate (13). Some of the reported deleterious effects on plants induced by salt stress include: a decrease in several metabolic processes such as respiration, photosynthesis, protein and nucleic acid synthesis in several plant species (32), a suppression of chloroplast development in bean (36) and a reduction in cytokinins translocation from the roots in tobacco (30). Salinity caused tomatoes (28) and barley (22) to accumulate more carbohydrates.

The difficulty in comparing tolerance in the different stages of plant development, due to the dissimilarity

of criteria employed in the evaluation of growth, prevented a single clear cut universal definition of "salt tolerance." It may be considered as the capacity of the plant to survive under conditions of increasing salinity stress. It might be evaluated either on the basis of the relative performance of the plant at a given level when compared with other plants or the performance of the plant at a certain salinity level relative to its behavior under non-saline conditions (27).

Salinity effects on plant development and yield might depend on such factors as: the plant species, the type of crop, stage of development and/or other related and interacting factors (12). Cereals (Hordeum, Avena and Triticum) are said to be less sensitive to salinity stress than legumes (Pisum Phaseolus, but more sensitive than other species such as Medicago, Helianthus and Beta (32). In the cereal group, barley was more tolerant than oats (5) and wheat (2, 5), while corn was the least salt tolerant cereal (26). Wild relatives of tomatoes were more tolerant than the cultivated ones (42). Phosphoenolpyruvate carboxylase enzyme isolated from leaves of C_4 plants appeared more sensitive to inorganic salts than the same enzyme extracted from C_3 plants (37).

Plant reaction to salt stress varied depending on the stage of its development (12). There might not be a positive correlation between salt tolerance at germination and during later phases of growth (3, 26). Sugarbeets, for instance, were more sensitive during germination than later growth phases (7, 12). On the other hand, corn (3, 12) and sesame (47) were more tolerant during germination than at later stages (3, 12).

The early seedling stage of most grains was more affected than either germination or later stages (7, 38). However, the four-leaf stage was the most sensitive stage in wheat and barley (2).

Selection in wheatgrass for salt tolerance in the germination stage was ineffective in increasing salt tolerance at subsequent growth stages (19). Furthermore, while salinity decreased markedly the vegetative growth of barley, the grain yield remained essentially unchanged (2), whereas the reverse appeared to be the trend in rice (12).

The adaptability mechanism may not be a capacity to function with large quantitites of salt within plant tissues (18), and it may not necessarily be the same in all species. The desert saltbush [Atriplex polycarpa (Torr.) S. Wats.] adapted to salinity by localizing the

absorbed salt in the trichomes, essentially isolating it from the mesophyll tissues (18). The adaptability mechanisms were reported to include passive exclusion or active extrusion, and dilution of the entering salt (18, 24, 32).

Significant varietal differences in salt tolerance of agronomic value have been observed in crops such as barley (1, 2, 3, 6, 26, 34, 35, 40), wheat (17), wheatgrass (19), rice (38), sugarcane (11), green beans (8), alfalfa (14) and tomatoes (33). The amount of variation in barley varieties was the most striking of all. California Mariout, for instance, a barley variety of Egyptian origin is widely known for its excellent salt tolerance during its entire growth period (1, 3, 26). In one study it gave 80% germination at the 0.3 percent salt level (26). Atlas (2, 35) and Regal (34) varieties were also highly salt tolerant. When irrigating with water containing 10,000 ppm salt, Atlas gave 96% grain yield of the control (2). Also, Palestinian, Eriterean and Ethiopian barley samples from collections at Rastov (USSR) were more resistant to salinity than those of European origin (40).

Although the physiology of tolerance of such superior varieties is not yet determined, it was reported

in one study that salt tolerant varieties of barley, translocated less sodium and chloride to the shoots than did a salt sensitive variety (24).

MATERIALS AND METHODS

The lack of a standard procedure to approach the problem of salt tolerance and to measure the various degrees of tolerance in barley brought about the need to first develop a practical screening technique. A satisfactory technique should be sensitive to a wide range of salinity levels and capable of measuring and identifying various levels of salt tolerance.

I. Preliminary Test

Thirty-three varieties of barley, native to several geographic locations and of various growth habitats, were selected for the study. There was no prior information on the salt tolerance of these varieties, except for California Mariout, a variety which was previously known to be salt tolerant. However, the varieties selected were assumed to represent a satisfactory range of germplasm adequate for the purpose of the study. The list and description of varieties are given in Table 1. A technique developed by

TABLE 1.--List of barley varieties screened for salt tolerance.

Variety Name	Identification	Source
Abed Mendor Brzz	not available	Denmark
Ackermanns Isaria Nova	PI 328618	Germany
Akan Mugi	CI 11225	Japan
Asa	Cl 11307	Sweden
Baladi	Cl 11187	Egypt
Barbless	Cl 5105	USA
Beecher	Cl 6566	Egypt
Bonus	Cl 11189	Egypt
Bruens Volla	Cl 11332	Germany
Bruens Wisa	Cl 10089	Germany
California Mariout	Cl 1455	Egypt
Carlsberg II	Cl 10114	Denmark
Coho	Cl 13852	USA
Conquest	Cl 11638	USA
Dickson	Cl 10968	USA
Domen	Cl 11417	Britain
Freja	Cl 7130	Britain
Giza 117	Cl 11190	Egypt
Heines Haisa II	Cl 10113	Germany
Ingrid	Cl 10083	Sweden
Lâjbjey Drosihezy A	not available	Denmark
Manchuria	Cl 2947	Manchuria
Mashu Mugi	Cl 11226	Japan
ND B134	not available	USA
Orge Martin 839	Cl 9266	Algeria
Orge Saida 183	not available	Algeria
Pallas	Cl 11313	Sweden
Paragon	Cl 13649	USA
Primus	Cl 13109	USA
Rika	Cl 11421	Britain
Rokkaku Ozeki	Cl 11227	Japan
Traill	Cl 9538	USA
Wadi Majanen	Cl 11211	Libya

Whitmore and Sparrow (45), originally designed for laboratory malting tests, was applied with some modification to fit the purpose of this test.

Six levels of salinity were chosen. Solutions of 4, 8, 12, 16, 20 and 24 thousand parts per million (ppm) sodium chloride were prepared by dissolving the equivalent amount of the salt in a proper volume of distilled water. A seventh treatment consisting only of distilled water was included as a check.

From the thirty-three varieties, eleven were picked at random for a preliminary test. To identify different varieties a sample of 240-270 kernels, selected for uniformity from each variety, was placed in a petri dish and the dorsal side of the kernels was sprayed with a thin coat of colored enamel, which, when previously tested was found to have no adverse effect on germination. A record was kept for the varieties along with their matching color.

For each treatment, 30 seeds from each variety were mixed and placed in a 100 ml beaker. A volume of 40 cc of treatment solution was poured into the beaker. The seeds were mixed thoroughly with the solution to prevent kernels

from floating. The beakers, with their contents, were placed in a growth chamber at 12°C for 48 hours. The treatment solution was changed every 12 hours. At the end of the 48-hour period the salt solution was filtered off and the wet kernels were gently mopped with paper towels. The seeds were then transferred to 15.0 x 2.5 cm test tubes. Corks, each with a 0.48 cm hole, were inserted and the test tubes were placed in an upright position in a growth chamber at 17°C for 6 days. On alternate days the germinating seeds were carefully removed from the test tubes, mixed to prevent rootlets from tangling together, and soaked for 3 to 5 minutes in the salt solution and replaced after removing the excess solution. The test was carried out twice. The test tubes with the germinating seeds are shown in Figure 1a.

The effect of salinity on seed germination was evaluated on the basis of the coleoptile growth. The coleoptile length relative to the length of the kernel was rated from zero to 8.[1] A zero rating designated no coleoptile growth, "1" equals 1/4, "2" equals 1/2, "3" equals 3/4 of the kernel's length and so on up to "8"

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[1] A standard technique.

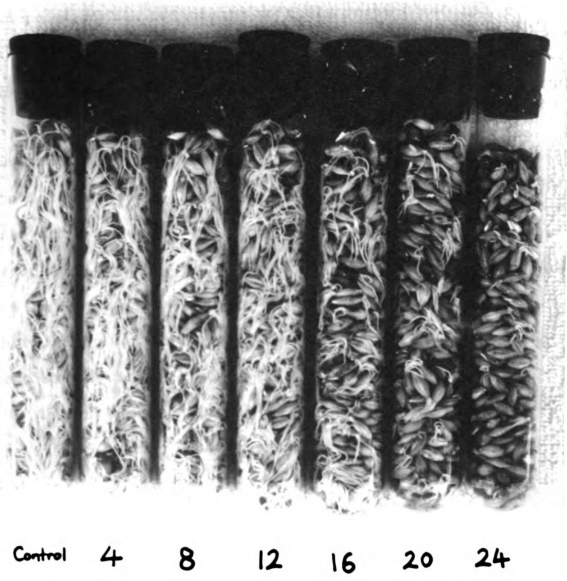

FIG. 1a.--Test tubes containing germinating barley seeds in several salt concentrations.

designating coleoptile growth as twice the length of the kernel. Coleoptiles were considered as extending from the mid-point of the coleorhiza to their respective tips.

II. Screening test (Germination Stage)

Based on the results obtained from the preliminary investigation, the 20,000 ppm salt level was selected for the screening test. The varieties were divided at random into three equal groups of 11 varieties each. In each group the varieties were identified as previously described and 30 uniform seeds from each of the 11 varieties were thoroughly mixed and placed in a 100 ml beaker. The kernels were soaked in 40 cc of the 20,000 ppm NaCl salt solution. The rest of the experiment was pursued as described in the preliminary test. This was repeated three times with a separate random regrouping of the 33 varieties prior to each replication.

III. Early Growth Stage Test

The purpose of this experiment was to test whether salt tolerance in the germination stage was correlated with tolerance in the early growth stage. Based on the

results of the screening test (in the germination stage), twelve varieties were chosen for this test. Of these varieties three were salt tolerant, three salt sensitive and the rest intermediate.

Standard plastic trays with air tight sealed lids, about 30.5 x 19.5 x 6.5 cm (Figure 1b), were adapted to this test. Seventy-two holes, slightly larger than 0.64 cm in diameter, were drilled in the tray lids. The holes were arranged in six rows of twelve holes each. The distance between holes was kept approximately equal. Trays and lids were sprayed on the outside with several coats of aluminum enamel paint to discourage algal growth.

A 10.5 x 0.64 cm transparent plastic tube (straw) was adapted to support the young growing plant. At about 2.5 cm from one of the tube's ends, two holes were punched using a paper punch. A cotton cigarette filter about 2.0 x 0.64 cm was inserted into the tube to a position, so that it did not entirely cover the holes: leaving a small opening that was big enough to allow root growth but small enough to keep the kernel from slipping through (Figure 1c). The size of the opening was increased as needed by carefully pushing down the filter to allow for

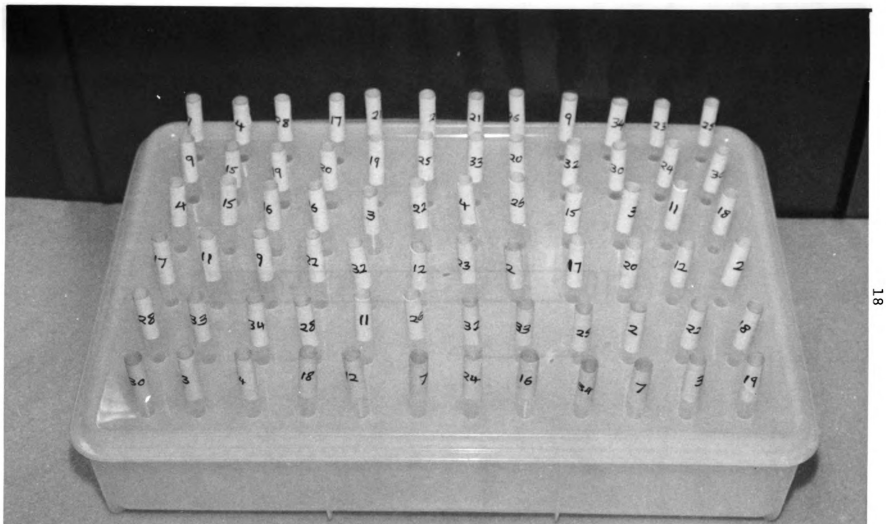

FIG. 1b.--A view of the tray used to grow plants in the nutrient solution.

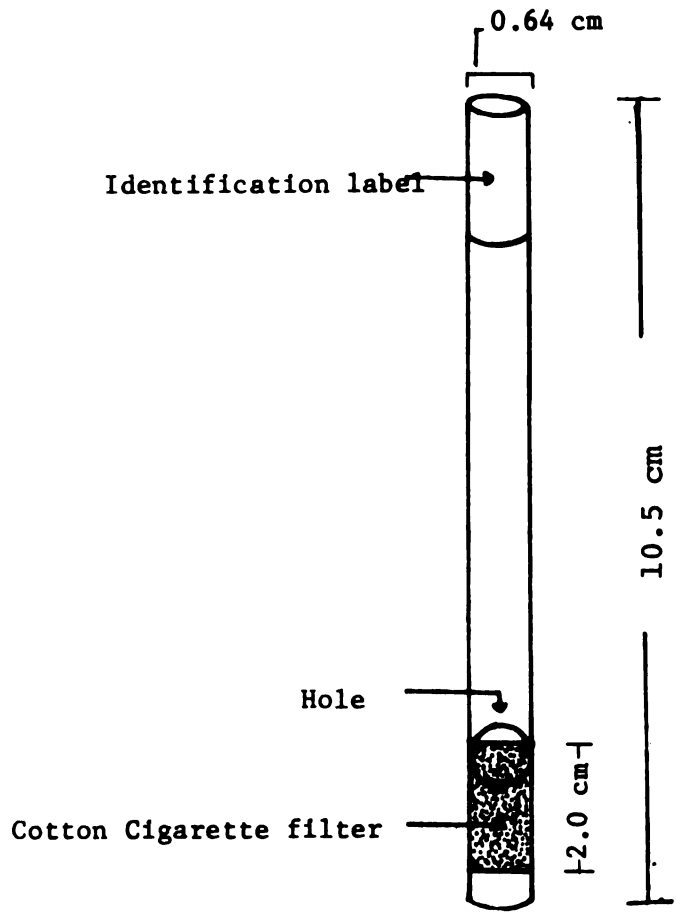

FIG. 1c.--A sketch of the plastic tube used to support plants in trays.

the root growth, The tip of the other end of the tube was wrapped with adhesive tape to identify individual plants.

A Hoagland's No. 1 nutrient solution was chosen as a base nutrient media and prepared two days before conducting the experiment. Its chemical composition is given in Appendix 1.

Sodium chloride was added to the basal solution to make three solutions of 3,000, 6,000, and 9,000 ppm NaCl. The NaCl-free basal solution was used for the control. The pH of all solutions was adjusted every four days to 6.5 $\pm$ 0.2 using 0.1N acetic acid and 0.1N ammonium hydroxide.

Seeds from each of the twelve varieties were marked and germinated in distilled water as described earlier. The germinated seeds were then gently placed in the individual tubes so that the young roots touched the cigarette filter which was moistened with distilled water prior to the placing of the seed. The mounted tubes were randomly allocated to individual holes on the tray lids. One liter of distilled water was poured in each tray, and trays were sealed with lids. After three days, when the first leaf was just emerging from the tube the distilled water in the trays was

drained and replaced by the treatment solution. The volume of the treatment solution was adjusted to one liter daily, by adding the appropriate volume of the treatment solution. In the last six days of the experiment, the solutions of the control and of the 3,000 ppm treatment were increased to 1.5 liters and kept so until the termination of the experiment as a result of the fast growth of plants in these treatments.

Experiments were repeated three times and conducted in the greenhouse and in the growth chamber. In the case of the growth chamber a temperature of 21 to 23°C and a 12 hour day were kept throughout the experiment. Bubbling compressed air for ten minutes every day provided sufficient aeration for good plant growth.

At the end of 18 days, when the majority of plants were at their four-leaf stage, individual plants were carefully removed from the tubes. Data on the height and total dry weight of the plants were gathered.

The data were expressed in all tests as percentages of the control to remove the effect of inherent germination and growth characteristics between varieties, and were then transformed using angular transformation (Angle=arcsin $\sqrt{\text{percentage}}$) prior to data analysis.

IV. Genetic Investigation

Results from the screening test, indicated that salt tolerance was a continuous rather than a discrete variable. For that reason the technique of the diallel-cross analysis, developed by Jinks (31) and Hayman (25) was found most appropriate for this study. Compared to other methods available the diallel-cross technique provided a more systematic approach to studies of continuous variation of data. The over-all analysis permitted extraction of reliable genetic information on dominance and on non-allelic interaction.

In this technique, all possible crosses, including selfing between a selected set of parents were made with assumptions that:

1) the parents were homozygous,
2) the inheritance was diploid,
3) genes at different loci were independently distributed in the parents,
4) no multiple allelism,
5) absence of maternal effects.

In the analysis the following second degree statistics were calculated:

1) the variance of parents (V_p),

2) the variance of the offspring of each parental array (V_r) and

3) the covariance of the offspring of each array with the non-recurring parent (W_r).

The regression of W_r on V_r was obtained and V_r was plotted against W_r.

Consistency of $(W_r - V_r)$ over arrays and the significance of the regression of W_r on V_r should jointly indicate the validity of the hypothesis postulated.

Consistency of $(W_r - V_r)$ was tested by using the formula:

$$t = \sqrt{\frac{r-2}{4}(\text{Var. } V_r - \text{Var.} W_r)^2 / \text{Var. } V_r \text{ x Var. } W_r - \text{Cov.}^2 (V_r, W_r)}$$

with r-2 degrees of freedom, r being the number of parents. Significance of t indicated failure of the hypothesis. Significance test of the regression of W_r on V_r was carried out by the formula:

$$t_1 = \frac{b-0}{s_b} \quad \text{and} \quad t_2 = \frac{1-b}{s_b}$$

where $s_b \sqrt{s^2_{y \cdot x} / \Sigma x^2}$ with r-2 degrees of freedom. Non-significance of t_1 indicated failure of the hypothesis, while significance of t_1 indicated the presence of dominance. The significance of t_2 indicated that non-allelic gene interaction was present.

On Mendelian grounds, the array of offspring of the most dominant parent would be the least variable array and should have the smallest variance and covariance. The opposite would be true for the array of offspring of the most recessive parent. The parabola $W_r^2=V_pV_r$, delimited the area in which coordinate data (W_r, V_r) must occur. The line of unit slope (b=1) through the origin and $\bar{V}_r$, $\bar{W}_r$ (where $\bar{W}_r$ was the mean of the covariances and $\bar{V}_r$ the mean of the variances) was the line of complete dominance. Movement of the regression line of unit slope upward relative to the line of complete dominance would denote partial dominance, while movement downwards would denote overdominance. Non-allelic interaction, if present, would move the line to the right and drop its slope below the expected value of unity.

For the diallel-cross, six parental varieties were selected. The varieties were: 1) California Mariout, 2) Lajbjey Drosihezy A, 3) Ingrid, 4) Coho, 5) Mashu Mugi and 6) Orge Saida 183. Based on the screening test, the first two varieties were considered salt tolerant and the last two salt sensitive.

The fifteen crosses of the 6 x 6 diallel were made in the greenhouse in the spring of 1975. F_1 seeds were grown to obtain F_2 seeds. The study material was confined to the F_2 seeds of the 15 crosses due to the difficulty of obtaining uniform and adequate F_1 seeds. Also any breeding program, excluding hybrid barley, would be dependent upon selection subsequent to the F_1 and test procedures should be applicable.

The F_2 seeds of the 15 crosses along with the six parents were tested for salt tolerance at the germination stage, in a 20,000 ppm NaCl solution as described earlier. The test was repeated three times. They were also grown in a Hoagland solution containing 9,000 ppm NaCl, to test for salt tolerance at the early growth stage. In each of six replications, three plants from each entry were grown to the four-leaf stage.

RESULTS

The purpose of this study was to acquire information on the inheritance of salt tolerance among a selected set of barley varieties.

In a sample of eleven barley varieties, the preliminary test results on the effect of the salt concentration gradient on the germination showed that increasing salt concentration significantly decreased germination as measured by coleoptile growth (Figure 2).

The regression analysis in Figure 2 shows that coleoptile growth and salt concentration entertain a strong linear relationship. The differences in responding to the salt concentration gradient among the barley varieties tested was supported by having different regression lines (Figure 3). Where the regression lines of two salt tolerant varieties Beecher and Lajbjey Drosihezy A, and of two salt sensitive ones Rika and Ingrid are shown. The mean value of the 11 varieties for both plant height and total plant dry weight decreased as salt concentration increased (Figures 4, 5, and 6).

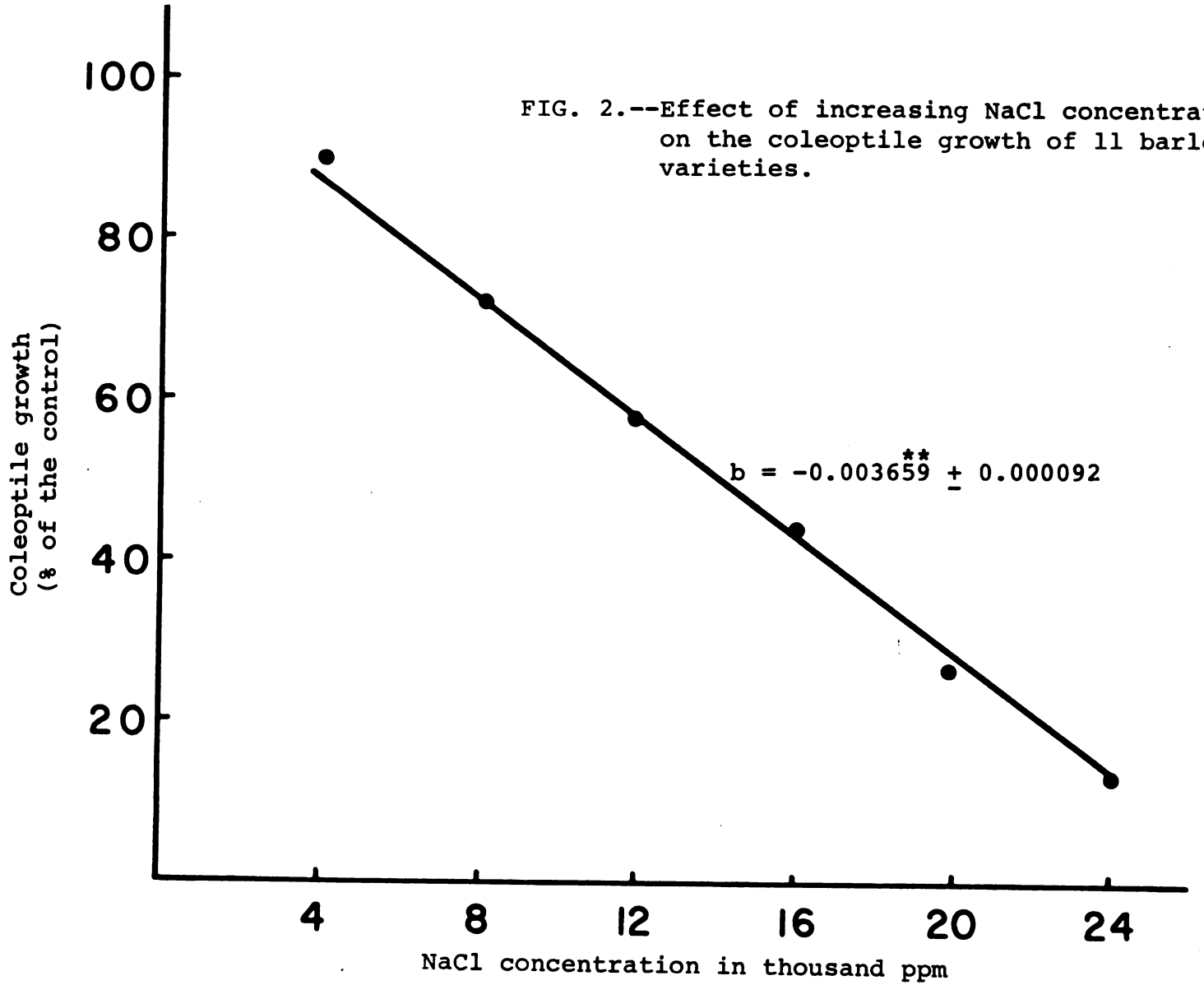

FIG. 2.--Effect of increasing NaCl concentration on the coleoptile growth of 11 barley varieties.

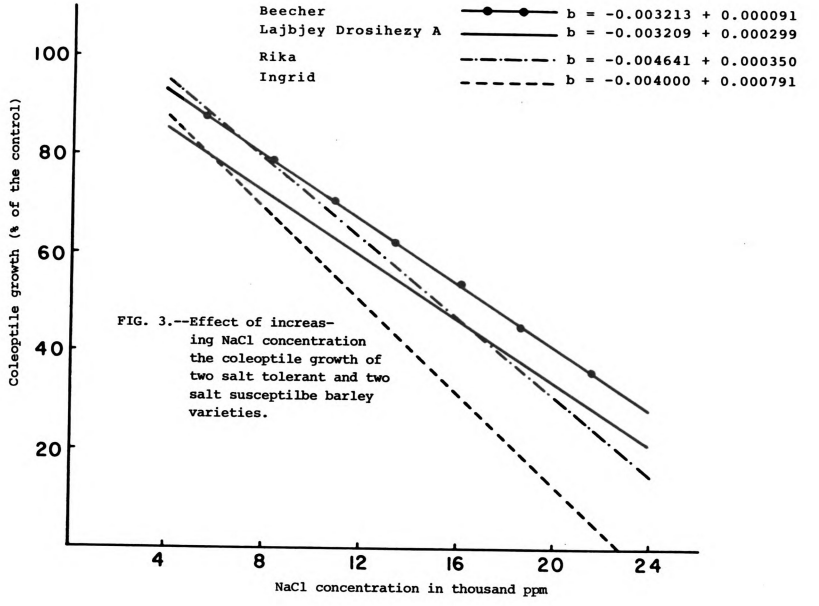

FIG. 3.--Effect of increasing NaCl concentration the coleoptile growth of two salt tolerant and two salt susceptilbe barley varieties.

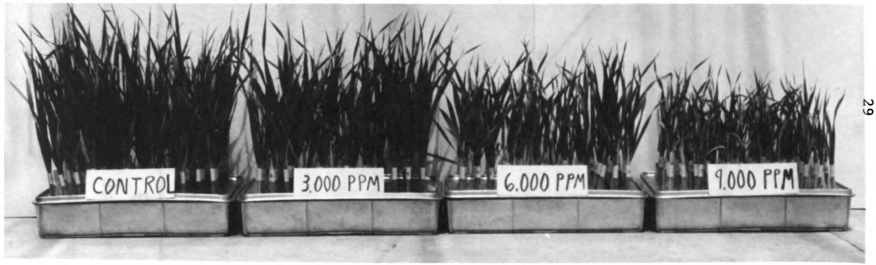

FIG. 4.--A view of nutreint tray in operation containing 12 barley varieties in solution with 0, 3000, 6000 and 9000 ppm NaCl.

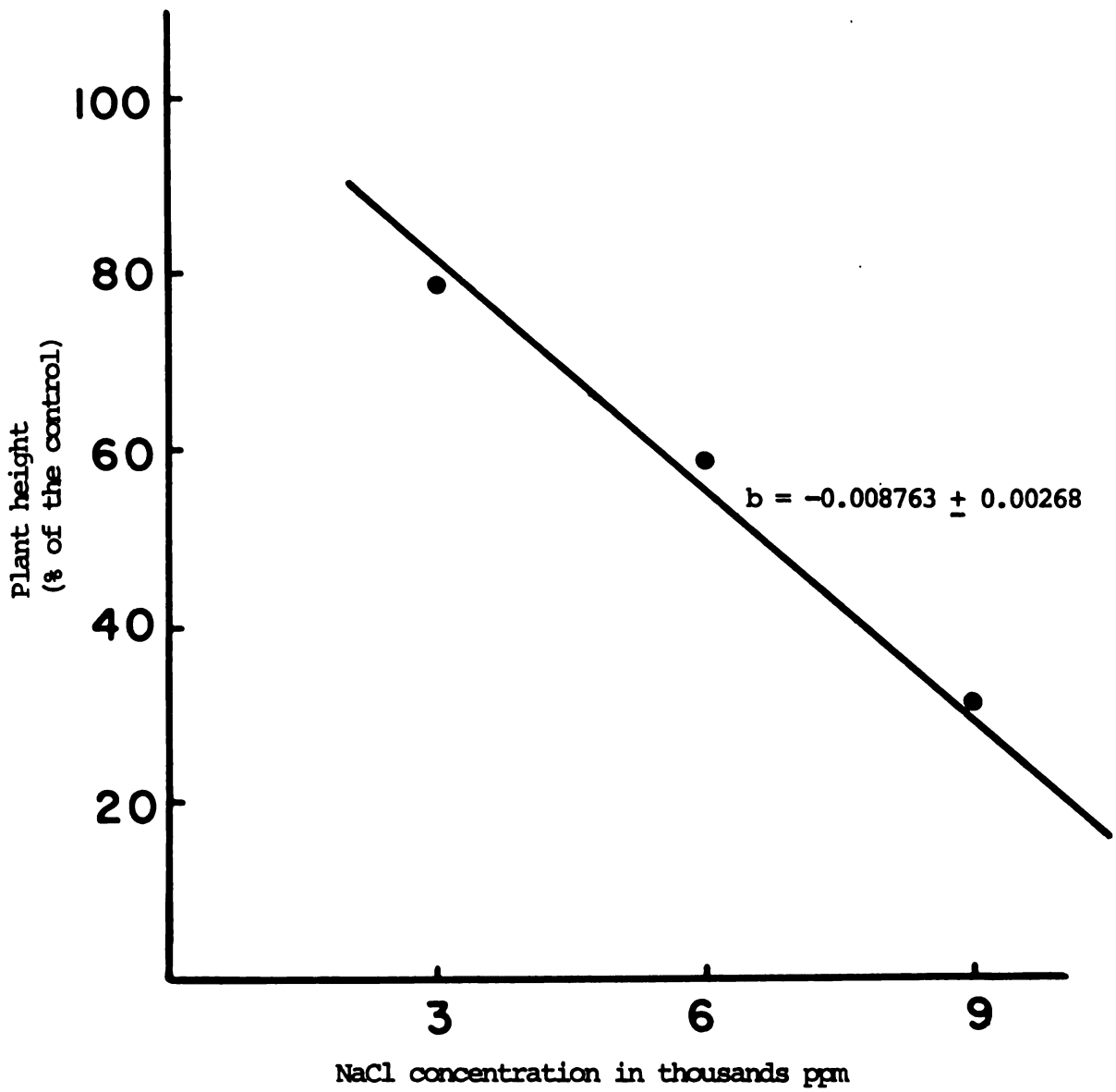

FIG. 5. Effect of NaCl concentration on the plant height of 12 barley varieties.

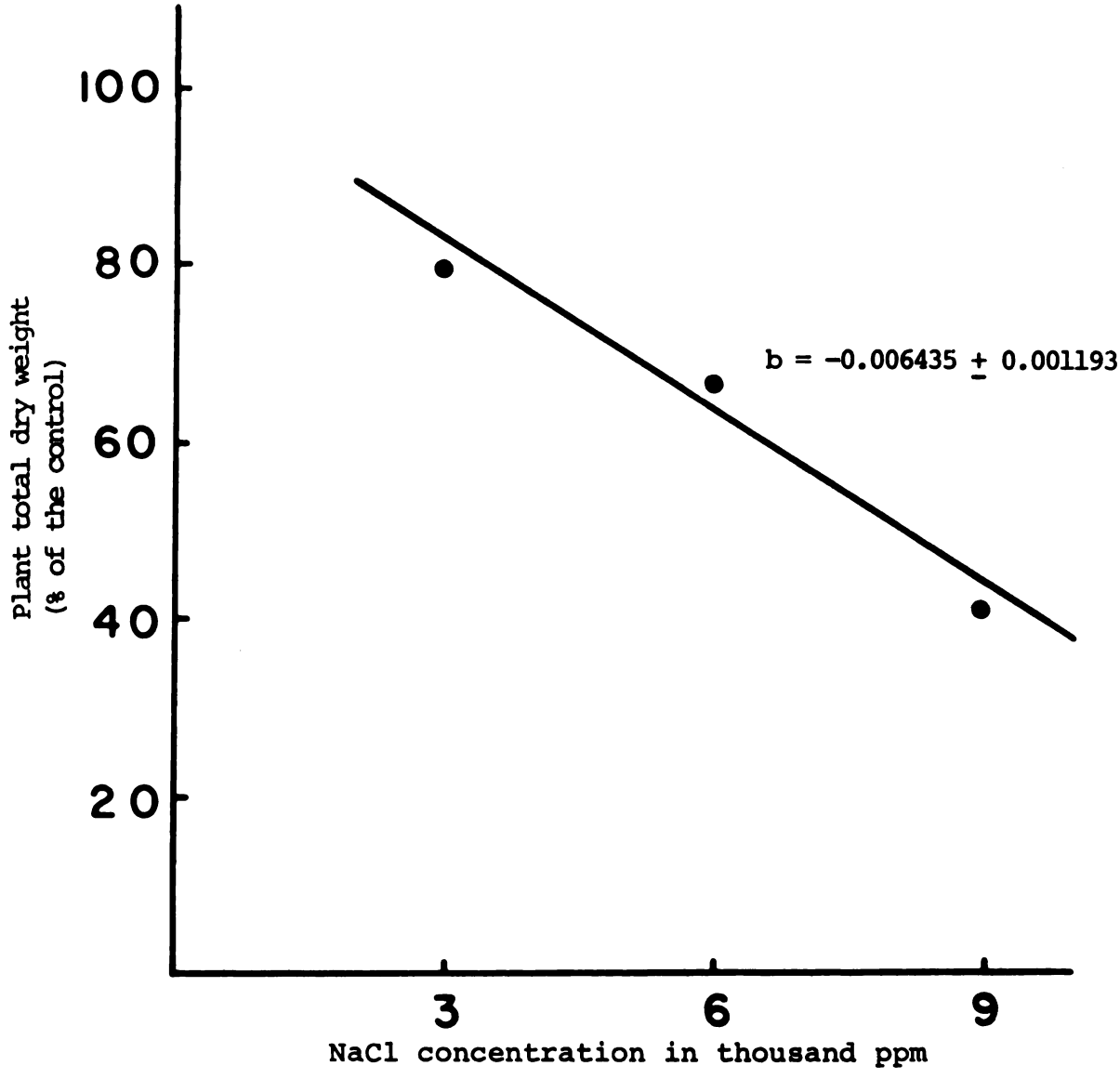

FIG. 6.—Effect of NaCl concentration on the total dry weight of 12 barley varieties.

The genetic investigation will be discussed on the basis of the results of the salt tolerance tests in the germination and the early growth stages on the F_2 progenies of the 6 x 6 diallel set. The diallel cross data is required to show a significant variation among hybrids for it to contain valuable genetic information. This step is usually examined prior to carrying on further analysis. The results of the analysis of variance of the six parents and their fifteen F_2 hybrid progenies for salt tolerance test at the germination stage is presented in Table 2.

TABLE 2.--Mean squares for salt tolerance score in the germination stage of the F_2 of the 6x6 diallel cross set.

Source of Variation	Degrees of Freedom	Mean Square	F
Blocks	3	3.5796	1.2071
Entries	20	72.3489	24.3969**
Blocks x Entries	60	2.9655	
Total			

**Significant at 1% level

A highly significant difference existed among entries. Consequently, the genetic relationship among this set of selected parents and progenies was analyzed using the technique of

Jinks-Hayman's diallel cross analysis and the graphical analysis were based on the variances and the covariances of the arrays.

The F_2 data of salt tolerance in the germination stage is summarized in Table 3. Each value is the mean score of 120 F_2 seeds. The array's variance (V_r) and covariance (W_r) are given in the right hand side of Table 3.

The table shows that the mean of the crosses generally lies in the range of the parents. The cross 2 x 3 had a value equal to that of parent 2 and two crosses 3 x 4 and 3 x 6 slightly exceeded both parents. The cross 1 x 3 had the highest score of all crosses. All these cases of discrepancies were associated with parent 3, a relatively intermediate variety in the scale of salt tolerance. The V_r values show that array 1 was the least variable and array 5 the most variable.

The t value for the test of the consistency of the variable ($W_r - V_r$) over arrays was calculated as t=0.4512 and found not to be significant ($p > 0.50$). The regression graph of W_r on V_r is shown in Figure 7 along with the limiting parabola $W_r^2 = V_p V_r$.

TABLE 3.--Salt tolerance score (% of the control) in the germination stage of the F_2 of the 6x6 diallel cross set.

Parental Number	Parents	1	2	3	4	5	6	Vr	Wr
1	California Mariout	48.94						13.1251	29.6252
2	Lajbjey Drosihezy A	41.63	43.47					31.5961	43.4218
3	Ingrid	44.58	43.47	31.83				50.2677	74.3327
4	Coho	41.37	33.19	32.35	28.51			36.5323	58.8350
5	Mashu Mugi	42.99	39.44	26.60	22.99	21.35		94.0452	111.1356
6	Orge Saida 183	38.17	30.15	33.83	30.93	20.93	20.08	51.4310	70.6425

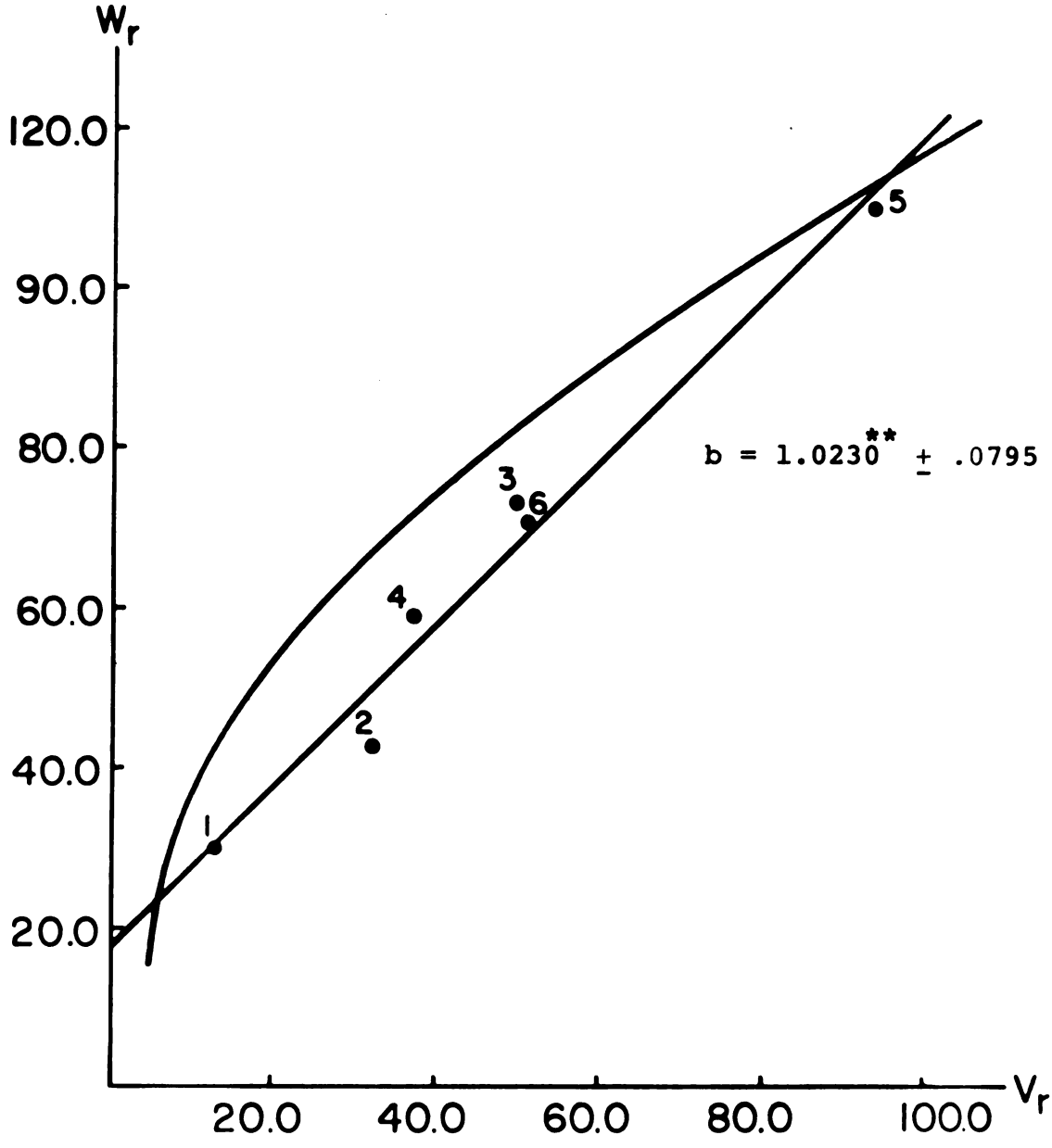

FIG. 7.--Wr/Vr graph analysis of salt tolerance scores in the germination stage of the F_2 of the 6 x 6 diallel cross set.

The graphical analysis shows that W_r and V_r enjoy an almost perfect linear relationship with regression coefficient $b=1.0230^{**} \pm 0.0795$, significantly greater than zero and practically equal to the unit slope.

The significance of the regression coefficient plus the uniformity of $(W_r - V_r)$ over arrays satisfy the assumptions underlying the theory of the diallel-cross analysis.

The graph shows that the most tolerant variety, parent 1 is at the dominant side of the regression graph, and parent 5, the least tolerant variety at the recessive side of the graph. This means that tolerance to salt was dominant, with parent 1 in this carrying most of the dominant genes and parent 5 carrying most of the recessive alleles.

From Figure 7, the regression line is shown to intercept the W_r axis above the origin ($\hat{Y}_o=17.4388^{*} \pm 5.5134$). Having found that $\hat{Y}_o$ is significantly greater than zero, it is said that dominance is partial rather than complete.

Since the data from the control were available and could be analyzed in the same way, it was thought useful to obtain information on the genetics of coleoptile growth

under conditions free from salt stress. This would enable us to understand the influence of the growth of coleoptile of the seed germinated under salt-free conditions on our measurements of salt tolerance in the germination stage.

The analysis of variance for the coleoptile growth of the 6 x 6 diallel set when seeds were germinated in a distilled water (control) is given in Table 4.

TABLE 4.--Mean squares for coleoptile growth score of the F_2 of the 6x6 diallel cross set.

Source of Variation	Degrees of Freedom	Mean Square	F
Blocks	1	0.2121	4.4103*
Entries	20	1.2596	26.1844**
Blocks x Entries	20	0.0481	
Total	41		

*,** significant at 5% and 1% levels respectively.

It shows a highly significant difference between entries. Table 5 summarizes the coleoptile growth scores for the six parents and progenies. Each figure is a mean of 60 seeds. The values of the array's variances and covariances were calculated and given on the right hand side of Table 5. A look at the table shows that the score of the cross exceeded

TABLE 5.--Coleoptile growth score of the F_2 of the 6x6 diallel cross set.

Parental Number	Parents	1	2	3	4	5	6	Vr	Wr
1	California Mariout	3.89						0.7285	0.5736
2	Lajbjey Drosihezy A	6.17	5.99					0.0949	-0.0448
3	Ingrid	4.66	6.61	4.13				1.2384	0.7497
4	Coho	5.35	6.15	4.65	4.26			0.7090	0.4619
5	Mashu Mugi	5.19	6.15	5.53	5.01	4.69		0.4172	0.3210
6	Orge Saida 183	6.02	6.77	6.81	6.41	6.32	5.08	0.4070	0.0040

in every case the score of the parent with the longest coleoptile. The lowest score was associated with the 3 x 4 cross, and the cross 3 x 6 gave the highest score. Both crosses involve parent 3 which has a relatively low score. Array 2 was the least variable array and array 3, the most variable one.

The graphical analysis is shown in Figure 8. The uniformity of ($W_r - V_r$) over arrays (t=1.5550) and a regression coefficient of W_r on V_r ($b=0.7452^{**} \pm 0.1591$) not significantly different from unity suggests that the data satisfy the assumptions of the theory of the diallel analysis. The distribution of parents on the diallel graph places parents 3 at the recessive side and parent 2 at the dominant side. From Table 5, parent 2 has a longer coleoptile than parent 3. This indicated that dominance was involved in determining coleoptile growth in barley and was directed towards the longer coleoptile. The regression line, however, intercepted the W_r axis below the origin suggesting over-dominance. When the W_r intercept was tested ($\hat{Y}_o=0.1023 \pm 0.0579$) it failed to be significantly different from zero. Therefore it was concluded that dominance was complete.

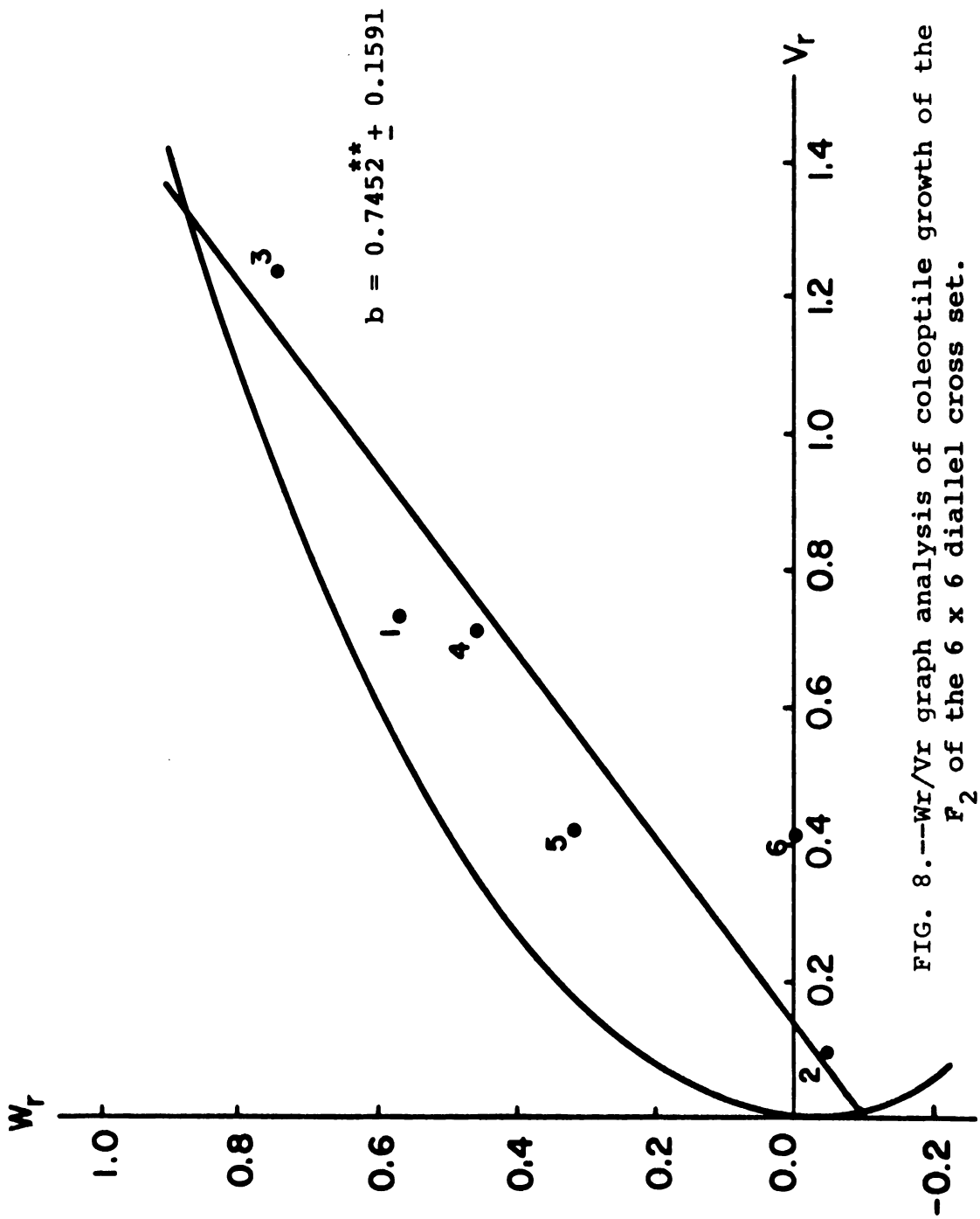

FIG. 8.--Wr/Vr graph analysis of coleoptile growth of the F_2 of the 6 x 6 diallel cross set.

The correlation between the salt tolerance score in the germination stage test for the progeny with mid-parent value for coleoptile growth in the control was r=-0.16 for 13 d.f.

Correlation Coefficients were calculated for each array with 4 d.f. between the salt tolerance score in the germination stage test of the offspring with coleoptile growth in the control for the non-recurring parent (Table 6). When they were converted to z values and averaged a non-significant r=-0.12 was obtained. It is also noted that the range in r values although quite large, the chi-square test for the homogeneity of the r values was not significant (x^2=1.6484), indicating no difference from an expected random sample of r values.

In order to investigate the relationship between salt tolerance in the germination stages and tolerance in the early growth stage, following germination and early seedling data from the early growth stage was subjected to the diallel and graphical analysis. Table 7 gives the analysis of variance for the 6 x 6 diallel set F_2 data. It shows a variation of significant value in the entries. The mean values of the plant's total dry weight of the F_2

TABLE 6.--Correlation coefficients between the salt tolerance score in the germination stage test of the offspring with coleoptile growth in the control for the non-recurring parent (d.f. 4) for each array.

Array	r
1	-0.61
2	+0.01
3	+0.21
4	-0.22
5	+0.09
6	-0.05
Average	-0.12
χ^2 for z values =	1.6484 ns

of the 6 x 6 diallel set are summarized in Table 8. Each figure is an average performance of 18 plants. The array's variances and covariances are given on the right hand side of the table.

Table 8 reveals that the performance of the crosses lies within the range of parents with few exceptions. For instance, the cross 2 x 3 exceeded the best

TABLE 7.--Mean squares for plant total dry weight in the early growth stage of the F_2 of the 6 x 6 diallel cross set.

Source of Variation	Degrees of Freedom	Mean Square	F
Blocks	5	19.3154	4.0611**
Entries	20	34.1937	7.1893**
Blocks x Entries	100	4.7562	
Total	125		

**significant at 1% level.

parent in the diallel cross set. While the crosses, 1 x 2, 1 x 3, and 2 x 5 fell below their corresponding parent with the low score.

The test for the consistency of the variable $(W_r - V_r)$ resulted in a non-significant t value of (t=0.7106). The graphical relationship of W_r and V_r along with the limiting parabola $W_r^2 = V_p V_r$ is given in Figure 9.

In the graph, points are scattered randomly around the regression line. This was further shown by the non-significance of the regression ($b=0.4991 \pm 0.2906$). Having found b not significantly different from zero violated the

TABLE 8.--Total dry weight score (% of the control) in the early growth stage of the F_2 of the 6 x 6 diallel cross set.

Parental Number	Parents	1	2	3	4	5	6	Vr	Wr
1	California Mariout	47.51						10.1298	17.1481
2	Lajbjey Drosihezy A	42.45	46.22					16.0769	12.5356
3	Ingrid	44.25	48.24	45.30				2.7711	5.6854
4	Coho	42.39	44.34	45.16	35.26			12.2515	13.0984
5	Mashu Mugi	42.10	37.64	44.84	41.31	40.61		7.8153	7.5716
6	Orge Saida 183	37.74	39.57	43.31	42.20	37.50	31.51	17.6588	13.3502

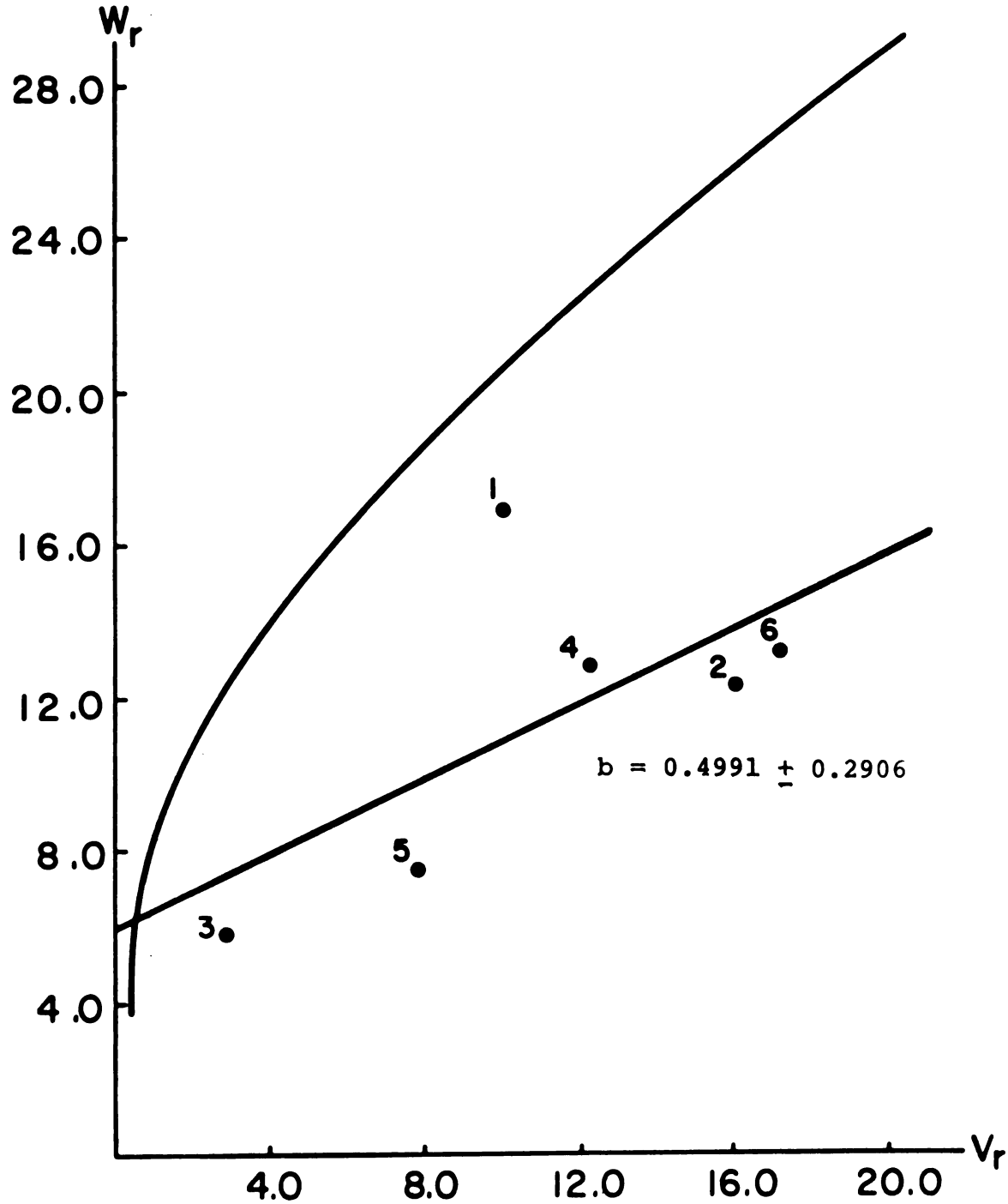

FIG. 9.--W_r/V_r graph analysis of the total dry weight in the early growth stage of the F_2 of the 6 x 6 diallel cross set.

assumptions underlying the diallel analysis theory. When analysis was done with parent 1 excluded the regression coefficient raised to ($b=0.6002 \pm 0.1433$) and became significantly different from b=0 and from b=1.0 (Figure 10). This new situation with b being between zero and one suggested that non-allelic gene interaction played a part in determining the control of salt tolerance at the early growth stage.

The W_r interception of the regression line fell above the origin ($\hat{Y}_o=4.8926 \pm 2.0178$). However, this value when tested, was not found to be significantly different from zero at the 5% level but greater than zero at the 10% level.

The examination of the distribution of arrays on the graph after removing parent 1 reveals that parent 3 and 6 occupy positions near the ends of the regression line. Parent 3 being in the dominant side and parent 6 in the recessive one. Since parent 3 had a higher total dry weight value that parent 6, it can be said that tolerance to salt at the early growth stage was also dominant, with the degree of dominance ranging from partial dominance to complete dominance.

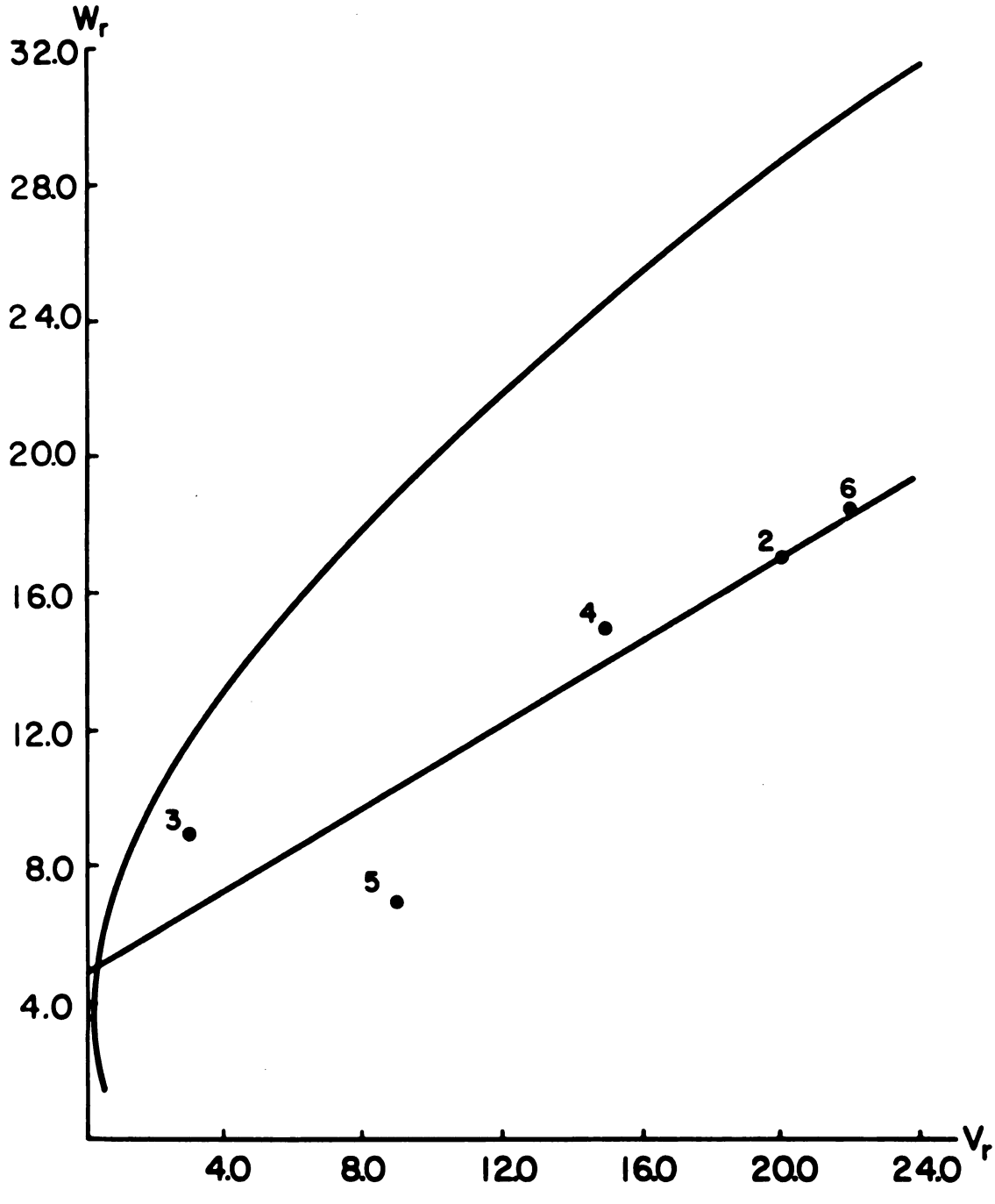

FIG. 10.--W_r/V_r graph analysis of Figure 9 with parent 1 eliminated.

In order to examine whether there was any relation between salt tolerance in the germination stage and salt tolerance in the early growth stage the correlation between the salt tolerance scores in the two growth stages was calculated for parents and crosses. The correlation for parents was $r=0.81$ with 4d.f. ($P < 0.1$) and for crosses was $r=0.28$ with 13 d.f. ($P > 0.2$).

When the two r values were averaged using the z transformation a non-significant $r=0.40$ was obtained. The chi-square test for the homogeneity of the r values ($\chi^2=1.867$) indicated that the two coefficients are not significantly different.

DISCUSSION

The adverse effect of increasing sodium chloride salt concentration on coleoptile growth in the germinating stage of barley seeds appeared to be linear. NaCl had a similar effect on the height and the accumulation of dry matter in barley plants grown to the four-leaf stage in nutrient media containing various concentrations of this salt.

The genetic investigation based on the Jinks-Hayman diallel cross analysis revealed that the assumptions underlying the theory of the diallel cross analysis were satisfied by the data of salt tolerance test in the germination stage of the F_2 of the 6 x 6 diallel cross.

The graphical analysis of the germination stage test (Figure 7), puts the most tolerant variety, parent 1, at the dominant side of the W_r/V_r regression graph and parent 5, a salt-sensitive variety at the recessive side. (Parent 1 originated in Egypt while parent 5 is from Japan.) This indicated that barley's tolerance to salt stress in

the germination stage seems to be determined by dominant genes. The regression line intercepted the W_r axis above the origin, suggesting that dominance is partial.

In the salt tests, the coleoptile growth, as a percentage of control was used in all analysis. When examining the growth rate of coleoptile per se of the controls, it too was found to be under genetic control (Table 5 and Figure 8). Dominance was complete and was in the direction of the longer coleoptile. Since the salt tolerance scores of the coleoptile growth were expressed as percentages of the control it may be argued that the higher salt tolerance scores obtained in the offspring of parents 1 and 3, both of which had a low coleoptile growth in the control, were an artifact of the use of percentages.

The average correlation between the salt tolerance scores in the germination stage test of the offspring with coleoptile growth in the control for the non-recurring parent (r=-0.12) plus the fact that the chi-square test for the homogeneity of the six r values was not significant (χ^2=1.6484) do not support such an argument. Although it should be pointed out that the correlation in array 1 was

relatively large (r=0.61), even though the average correlation for all arrays was near zero.

The diallel analysis indicated salt tolerance is dominant and further that parent 1 was at the dominant end of the diallel graph. Dominance coupled with a genetic tendency towards a low growth could be expected to produce negative r value when the offspring values within array are compared with the coleoptile growth rates of the non-recurring parents. However, since the coefficient in question is not significant plus the fact that the population of coefficients is homogenous and tend towards zero leads one to believe that the use of percentage values is valid. There seems no other way to measure salt tolerance (using growth rates) to eliminate or reduce the general effect of genetic differences in growth rate per se between cultivars. In retrospect it would seem that perhaps one could investigate half-life as an alternative measure, but this would be more difficult to do.

The regression analysis (Figure 9), shows that the structure of the F_2 data of the 6 x 6 diallel cross of salt tolerance test at the early growth stage, as distinguished from the germination test, did not quite meet the assumptions

demanded by the theory of the diallel cross analysis. The higher combining ability of parent 1, indicated by its high W_r value and by its location on the regression graph relative to other parents, suggests that parent 1 played a major part in the data's deviation from the expected linearity. When the analysis was repeated, with parent 1 eliminated (Figure 10), the regression coefficient increased to a significant level from $b=0.4991\pm0.2906$ to $b=0.6002^{*}\pm0.1433$.

The distribution of parents on the regression graph puts parent 3 on the dominant side and parent 6 on the recessive side of the graph. Since parent 3 scored higher than parent 6 in the salt tolerant scale in this growth stage, it was interpreted as barley's tolerance to salt at the early growth stage was also controlled by dominant genes. The regression line of Figure 10 intercepted the W_r axis in a point slightly above the origin suggesting that the degree of dominance was between partial and complete dominance.

The regression coefficient b, being significantly different from both zero and one, indicated that non-allelic gene interaction played a role in determining the

control of salt tolerance in this growth stage. Parent 3 a semi-tolerant variety, ranked third in salt tolerance among the six diallel parents in both the germination stage and the early growth stage. Parent 6 was the least salt tolerant of the parents in both growth stages.

Parent 3 originated in Sweden where salinity stress is probably not as agriculturally important as it is in Algeria where parent 6 originated. The most and the least salt tolerant varieties of the six diallel parents, in both growth stages are common to the North African region; where screening for salt tolerance over a long period of time is expected.

In spite of the fact that parent 3 has shown an intermediate degree of salt tolerance in both tests, the most tolerant hybrid in the germination stage (1 x 3) and the most tolerant hybrid in the early growth stage (2 x 3) both involved parent 3.

Although the correlations between salt tolerance scores in the two-growth stage were not significant in either parents or crosses and were not significantly different, the r value for crosses with 13 d.f. was relatively small (r=0.28) compared with the r value for parents

with 4 d.f. (r=0.81) which is near the edge of significance at the 5% level (t=2.723).

The biological conditions which led to such a small r value in crosses while a relatively high r value in parents are not at all obvious. The following hypotheses are introduced for discussion.

If salt tolerance in the two growth stages involved two separate gene systems the correlation of the two salt tolerance scores in the partially heterozygous F_2 progeny is expected to be influenced by differences in the degree of dominance in the two growth stages while the correlation of the two salt tolerance scores in the homozygous parents is free from dominance effect. The absence of strong evidence of separate gene systems reduces the validity of such a hypothesis. Given the facts that salt tolerance readings were not made on the same F_2 genotypes in the different growth stages and since the sample size was also different, (120 F_2 seeds in the germination stage vs 18 plants in the early growth stage), and the fact that heterozygosity in the F_2 population was relatively high, it is not unlikely for a situation like this to stem from a sampling error. It is expected that selfing the F_2 progenies for a few

more generations beyond the F_2 would fix most of the genes and result in a significant positive correlation between salt tolerance in the two growth stages.

In completing the discussion of the results of the genetic inquiry of salt tolerance in barley some remarks are in order. Firstly, all the tests regarding salt tolerance were confined to a single salt, namely sodium chloride. Thus the possibility that other gene systems may surface if other salts (single or combined) are used as the stress element cannot be ruled out. Secondly, plant growth is a continuous process and stages of growth often overlap with no distinctive boundaries between sequential stages. Therefore, reference to growth stages in this manuscript is rather artificial and done so only for convenience. Thirdly, the interdependency that characterizes some growth stages may result in salt tolerance or salt sensitivity in one growth stage influencing and/or depending on tolerance or sensitivity in the proceeding growth stage or stages. Finally, there is no current evidence that the investigated growth stages are, necessarily, the most critical stages in determining barley's overall tolerance to salt. We do know, however, that a seed must

germinate before a crop can be harvested and so germination is one critical stage.

More related information on the subject of salt tolerance is undoubtedly needed to expand our knowledge of the genetic basis of salt tolerance in barley.

SUMMARY AND CONCLUSION

This study acquired information on the genetic basis of salt tolerance in barley.

The germination stage test indicated that salt tolerance in barley appeared to be governed by genes possessing partial dominance. Parent 1 seems to possess most of the dominant genes and Parent 5 most of the recessive alleles. The best combination was the cross 1 x 3. Genetic control of salt tolerance seemed somewhat different as the plant growth stage advanced. The early growth stage test revealed that salt tolerance at this growth stage was controlled by dominant genes. Dominance appeared to be near complete. Parent 3, seemed to possess most of the dominant genes and Parent 6, most of the recessive alleles. The most tolerant combination in the early growth stage from the six parental diallel-cross was the cross (2 x 3), which surpassed even the best parent in the set. Non-allelic gene interaction appeared to play a role in determining the inheritance of salt tolerance in this growth stage.

The degree of tolerance was found to be somewhat consistent in the two growth stages in the parents, and not so in the crosses. This was attributed most probably to the differences in sample sizes in the two stages and to the heterozygous nature of the F_2 population.

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APPENDIX

APPENDIX 1. The Hoagland's No. 1 nutrient solution used as the basic nutrient media to grow barley plants to the four-leaf stage.

Six stock solutions were prepared separately as described below by dissolving in distilled water the designated amount of the chemical compound and then bringing up the volume of the solution to one liter.

Stock Solution No.	Concentration per Liter	
1	1 M	KH_2PO_4
2	1 M	KNO_3
3	1 M	$Ca(NO_3)_2$
4	1 M	$MgSO_4$
5	26.3 g	Fe chelate
6	2.86 g	H_3BO_3
	1.81 g	$MnCl_2.4H_2O$
	0.22 g	$ZnSO_4.7H_2O$
	0.08 g	$CuSO_4.5H_2O$
	0.016 g	MoO_3

To prepare one liter of the basic nutrient solution the specified amounts from each stock solution were added to 985 ml of distilled water as follows:

Stock Solution No.	ml/liter
1	1
2	5
3	5
4	2
5	1
6	1