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A GENETIC STUDY OF SALT TOLERANCE IN BARLEY (*HORDEUM VULGARE* L.)

By

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ABSTRACT

A GENETIC STUDY OF SALT TOLERANCE

IN BARLEY (HORDEUM VULGARE L.)

by

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Six varieties of barley of different origin were used to show the effect of salt on germination stage and mature-plant stage. A 6 X 6 diallel cross was made to study the genetic basis of salt tolerance during germination stage using Jinks-Hayman diallel cross analysis.

Varietal differences for salt tolerance were obvious in both stages of growth. There was no correlation between germination stage and mature-plant stage for salt tolerance suggesting the possibility of the presence of at least two sets of genes.

The genetic study, using F_3 populations, indicated the presence of two different genetic systems for salt tolerance in barley. One was found in California Mariout, in which salt tolerance is controlled by recessive genes. The second was found in the rest of the varieties in which the tolerance is controlled by dominant genes.

To my parents.......

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INTRODUCTION

Soil salinity is common in some arid and semi-arid regions of the world where rainfall is insufficient to leach the salt out of the root region. Soils severely affected can easily be recognized by a thin layer of white powdery material covering the soil surface.

Chloride, sulfate, carbonate and bicarbonate salts of sodium, calcium, magnesium and potassium are generally found in saline soils. The concentration of these salts varies from one region to another. These salts have a high degree of solubility in water which makes them easily removed from rocks and soils by erosion. Due to this process, irrigation water may be high in salt content and become a major source of salts added to the soil.

Problems develop from salts already in the soil, especially in arid and semi-arid regions where salts accumulate under certain environmental conditions. One is soil structure in which a layer of clay lies at various depths beneath the surface developing a poor drainage system in the soil. As a result, a salt solution would not penetrate through this layer and salt accumulates. Another factor is a high ground water table which provides a poor drainage system. In either case, water will not penetrate this layer. Capillary movement might carry the salts to the soil surface or allow lateral movement. As the water reaches the soil surface, it evaporates, leaving the salts to accumulate near the plant root zone.

High salt content in the soil reduces the availability of water to the plant as the osmotic pressure within the rooting medium increases and becomes higher than that in the plant tissues. It also affects the nutrient uptake by the plant. As a result, plant growth is reduced significantly causing a drastic reduction in yield.

Farming this kind of land becomes nonprofitable and leads farmers to leave their land since reclamation and maintenance are very costly.

With the increase in the population of the world and the demand for food, agricultural land has become too valuable to lose. Some farmers have become aware of this fact and started to grow salt tolerant species.

According to studies in this field, salt tolerance was found to be a heritable characteristic in plants. Proper breeding programs then should be effective in developing or improving some important economic crops. Extensive research is definitely needed to keep the salt concentration down to a level where a profitable farming system could be attained.

To study the tolerance of plants to salt, all stages of growth should be considered since the reaction to salt might be different from one stage to another. This study investigated the characteristics of salt tolerance in barley plants (*Hordeum vulgare* L.) during germination and later stages of growth.

REVIEW OF LITERATURE

A saline soil is one with sufficient soluble salts to injure or reduce the growth of many plants. Irrigation water is a major factor in causing salinity problems. Depending on the geological structure of the soil through which streams and rivers pass, different water has different salt content. Allison (5) reports that most irrigation waters contain 0.1 to 5 tons of salt per acre-foot (70 to 3500 ppm). He classifies irrigation water on the basis of electrical conductivity measurements into four classes: Low salinity, medium salinity, high salinity, and very high salinity, the dividing points between classes being 250, 750, and 2250 μmho/cm. This range includes water that can be used for irrigation of most crops on most soils to water harmful to use for irrigation under ordinary conditions.

In a given soil, the cations calcium, magnesium, and sodium and the anions chloride, sulphate, bicarbonate, and carbonate are generally predominant (5, 17). Potassium occurs but in lesser proportions than any of the cations mentioned (5). Proportions of these ions may vary considerably among saline soils. Addition of fertilizers may cause an increase in the variety of ionic species present in excess (17, 39). The presence of these salts in the soil causes the osmotic pressure of the soil solution to rise high enough to create a water stress condition. The osmotic pressure within the root hairs of most plants is usually about 2 bars (40). In saline soils, the osmotic pressure may rise far beyond 2 bars, and unless plants adjust to the osmotic pressure within their root hairs, they would not survive. Berstein (13) provided evidence that the water adsorption capacity is relatively unaffected by salinity. He related the reduction in plant growth associated with osmotic stress to building up of the osmotic pressure of developing cells to meet the increasing osmotic pressure of the rooting medium and still maintain turgor. He then defines salt tolerance according to his theory as, "the degree to which osmotic adjustment can be made without sacrifice to growth". It was reported earlier, however, by Eaton (27) that as the salinity of the medium increases, the osmotic pressure of the leaves or aboveground parts of the plant increases. This results in the maintenance of essentially a constant gradient between medium and plant. Hayward and Spurr (34) measured the rate of entry of water into corn (*Zea maize*) roots under different osmotic pressures. A significant reduction in the rate of entry was found in both non-conditioned and pre-conditioned plants to high osmotic concentration of the substrate. Seeds of alfalfa (Medicago sativa) showed a reduction in hydration as the concentration of the substrate increased with either sodium chloride or mannitol (49).

Efficiency of water use is also affected by salinity. The water requirements of wheat and saltbush decreased as the salinity increased, i.e., less water was used per gram of dry matter produced (26). In contrast, in a later study, Eaton (27) noticed an increase in water use for mixed culture of eight crops at higher levels of salinity than at moderate levels. This probably was due to accumulation of additional salts in plant tissue which might have led to the uptake of more water.

The osmotic pressure concept in describing plant growth depression is predominant in the literature. Plants in different studies were exposed to different levels of artificial osmotic pressure using mannitol and some other salts. Isosmotic pressures induced by mannitol and salts seem to have different effects on plant growth. Uhvits (49) using Arizona grown Chilean alfalfa seed, observed that germination percentage was reduced much more in sodium chloride than in mannitol at equal osmotic pressures.

Different salts may have different effects on plant growth. Gauch and Wadleigh (30) showed that sodium chloride, calcium chloride, and soidum sulfate at isosmotic concentrations had similar effects on the growth of red kidney bean plants (*Phaseolus vulgaris* L.), whereas with magnesium chloride and magnesium sulfate, growth was depressed markedly. This brings out the effect of specific ions. Kofranek *et al*. (39), in greenhouse operations, noticed that heavy application of fertilizer developed a specific ion effect on the growth of chrysanthemum (*Chrysanthemum morifolium*) associated with high levels of ammonium or magnesium salts. In both studies, magnesium as the specific ion provided additional depression in plant growth.

Higher concentrations of magnesium in the soil may cause toxicity to the plants (35). This effect, however, can be overcome if a moderately high concentration of calcium and potassium are present in the soil. Excessive concentrations of calcium, on the other hand, may depress the uptake of other cations.

Bernstein and Ayers (15) in studying the salt tolerance of five varieties of carrot (*Daucus carota*), noticed that at a given level of salinity using sodium chloride and calcium chloride, the sensitive varieties accumulated more calcium but less potassium. Hayward and Wadleigh (35), on the other hand, found that the presence of excessive sulfates decreased the uptake of calcium but promoted the uptake of sodium. As a result, sodium toxicity was induced (20).

Fruit crops are found to be very sensitive to sodium. Sodium injury in almonds was found in non-saline soils containing less than 5 percent of exchangeable sodium (17). Toxicities, of sodium and chloride ions, however, were considered as major factors in salt damage to specifically sensitive fruit crops.

Chloride is one of the major anions found in saline soils. It occurs in the form of salts with the cations sodium, calcium, and magnesium. It may be present in traces up to a few m.eq./1. in non-saline soils to about 100 m.eq./1. in saline soils (13, 14, 15). Under saline conditions, plants may accumulate up to 150 m.eq./100 gm or more chloride in their leaves. Allison (5) reports that chloride may accumulate to about 1 or 2 percent of the dry weight when the concentration in the root medium ranges from 700 to 1500 ppm. At those concentrations, plants show toxicity symptoms in which marginal burn of the leaves occurs, causing leaf drop, twig die-back and even death of the plant.

Chloride was found to have little or no effect on the uptake of the essential anions phosphate, nitrate, and sulphate even at high concentrations (3000 ppm) in the rooting medium (45).

Brown et al. (20) found that stone-fruit trees take up about twice as much Cl^- per m.eq. of Cl^- in the nutrient solution from calcium chloride than from sodium chloride. It was reported earlier, however, that the uptake of chloride from added calcium and sodium chlorides was found to be equal for most plants studied.

The mechanism of salt tolerance in the case of Na may be based on the particular plant or species to keep the proper Na level, in the leaf tissue below toxic levels and compensating for the lower water potentials associated with salinity by increasing levels of organic solutes in the tissue (46). Scholander, *et al*. (47) and Atkinson, *et al*. (6) have shown two different mechanisms of salt tolerance in taxonomically diverse mangroves. The first is concerned with excluding the salt in seawater by the roots: this was found in *Rhizophora* and *Bruguriera*. The second involves taking up the salt and excreting it by special glands on the leaves before toxic levels are reached in the shoot, examples: *Aegiceras*, *Aicennia* and *Aegialitis*. In a study involving six clones of *Festuca rubra* and four of *Agrostis stolonifera*, tolerance was associated with the restriction of Na^+ and Cl^- accumulation in the shoots and the maintenance of almost constant concentrations in the roots over the salinity levels of 0, 25%, 50%, and 75% seawater (32). This might be in favor of the excluding theory since the tolerant *festuca* clones were considered as an effective excluder at both low and high salinities.

Much of the research done on salt tolerance in plants has been during germination and early growth stages (1, 8, 12, 21, 22, 23, 24, 36, 44, 48). Soil salinity seems to have a significant effect on plant growth in general. It decreased the percentage of germinating seeds, increased the time of germination, and delayed the emergence of seedlings. Donovan (24) found that barley seeds required an additional 3-5 days to germinate in a saline culture. Maliwal and Paliwal (42) also stated that germination percentage of wheat (*Triticum aestivum*) and barley at different salt concentrations increased slowly with time. Increasing the concentration of salt in soils during germination resulted in decreasing germination followed by an increase in percentage of plant mortality (1, 22). Removing the salt at any time during the germination period, restored normal growth rates (29). Seeds of sugarbeets (*Beta vulgaris*), which failed to germinate but remained viable in a saline soil during an entire summer, germinated to produce normal seedlings the following fall when rains leached the salts from the vicinity of the seeds (18).

Most plants seem to be more sensitive to salt during the seedling stage than during other stages of growth.

This may be because the tissues are tender and roots are shallow (40). Dumbroff and Cooper (25) found that osmotic stress was most deleterious to tomato plants (Lycopersicon esculentum) when applied during early growth, especially during the succulent seedling stage. Rice plants were found to be much more sensitive during the seedling stage than during germination at a given salinity level (44). Reports on other crops all support this fact. The variation in tolerance to salt during germination and seedling stages is insignificant in practice especially under high salinity levels where plants can make it through the germination stage, but fail to pass the seedling stage (44).

Excess salinity reduces both rates of growth and total plant size. Forage and seed yield are usually reduced (40, 1). Increasing salinity levels in soybeans (Glycine max) increased plant mortality, and leaf necrosis. It also reduced green leaf color, leaflet size, dry stem production, plant height, seed yield and decreased seed quality, as would be expected as excess salinity increased accumulation of chloride in stems and leaves (1). Growth of most plants tested under saline conditions showed similar responses except for leaf color which darkened under increasing salinity, in the case of barley (9), alfalfa (19) and beans (30).

The degree of salt tolerance differs widely between plants. Barley was found to be a salt tolerant crop even at high salt concentrations. Ayers and Hayward (9) reported that "California mariout" barley germinated fairly well at high salt concentrations. In addition, they found that sugarbeets germinated poorly, and kidney beans did not germinate at all at moderate salt concentrations. Similarly, George and Williams (31) also found that "California mariout" germinated at higher salt concentrations compared to strawberry clover (*Trifolium fragiferum*) and Ladino clover. In other tests, barley was also found to be more tolerant than wheat (42) and oats (*Avena sativa*) (10).

Plants may have different degrees of salt tolerance during their growth stages (12). Sugarbeets are very tolerant to salt during the latter stages of growth, but are extremely sensitive to salt during germination. On the other hand, barley was found to be tolerant of salt during all stages of growth, although it was more sensitive during germination than at later stages (7). Barley plants grown under saline conditions have shown a decrease in vegetative vigor as evidenced by shortening of stems and decreased straw weights while maintaining essentially full yields of grains (9). Rice (*Oryza sativa*) plants were found to be more tolerant of salt during germination than during the seedling stage (2, 3, 38, 44). Tolerance of rice seedlings to salt showed an appreciable increase at six-weeks of age (39). This increase in tolerance seems to cease later. The same study showed that these plants developed essentially normal straw yields but produced little or no grain.

The degree of salt tolerance differs not only between plants, but also among species and varieties. Wheat varieties showed different responses at different levels of salinity during germination (11). A decrement of 50% in germination of a sensitive variety was found at a salinity level of -16 atm., while the tolerant variety showed the same decrement but at a salinity level of -20 atm. In tomatoes, Rush and Epstein (46) indicated that Galapagos ecotypes were more tolerant than the esculentum cultivars. Abel and Mackenzie (1), worked on soybeans, and noticed that tolerant varieties under saline conditions had little or no leaf necrosis, compared with other intermediate salt tolerant varieties. They then suggested the presence of inheritance factors for salt tolerance. Maddur (41) stated that salt tolerance in barley was carried out by partially dominant genes during germination and partial to complete dominant genes during early growth stages. Donovan (24) related differences in salt tolerance to the differences in the imbibitional ability and a selective permeability of the seeds and/or the coleoptile epidermis to salt. Hunt (37) worked on intermediate wheatgrass and found that salt tolerance was a highly heritable characteristic. He found a great deal of variation between clones during germination and seedling stages. He also found that selection within species of tall wheatgrass produced greater salt tolerant strains.

In another study, Dewey (22) also stated that selection in salt tolerance could be effective on crested wheatgrass (*Agropyron cristatum*) to obtain a salt tolerant strain. However, selected wheatgrass plants from germination tests did not show an appreciable improvement when planted in the field (23). F_1 hybrids of two varieties of rice showed high resistance to salinization when compared to their parents for number of spikelets per panicle, panicle weight and grain yield per plant (4).

The character of salt tolerance can be found in the wild relative species of some crops. A successful attempt was made to introduce this characteristic to the cultivated tomato plants, from the Galapagos salt-tolerant wild species *L. cheesmanii* (28).

A salt tolerant plant species or variety does not mean that it will tolerate salt throughout it's life just because it has a good tolerance during the germination period (8). Hunt (37) found little or no correlation between salt tolerance of intermediate wheatgrass during the seedling stage and later growth stages. Abel and Mackenzie (1) also noticed in soybeans that salt tolerance during germination and in the later stages was not apparently related. Barley cultivars showed different responses throughout their life cycle (43). One cultivar coped with high salt stress at emergence but did not make the transition into the vegetative phase under high stress. Another cultivar, on the other hand, showed the opposite reaction. This may suggest the presence of two sets of genes for each stage.

MATERIALS AND METHODS

Six varieties of barley previously selected by Maddur (41) according to their degree of tolerance to salt at germination stage. Their local names, identification, source and degree of tolerance to salt are given in Table 1.

TABLE 1. Barley varieties that were used in this study.

Variety Name	Identification	Source	Degree of Tolerance
California Mariout	CI 1455	Egypt	Tolerant
Lajbjey Drosihezy A	not available	Denmark	Tolerant
Coho	CI 13852	USA	Moderate
Ingrid	CI 10083	Sweden	Moderate
Mashu Mugi	CI 11226	Japan	Sensitive
Orge Saida 183	not available	Algeria	Sensitive

I. Screening test at germination stage:

A screening method similar to the one developed by Whitmore and Sparrow for Laboratory malting (50) was applied with some modifications to fit the purpose of this study.

Seeds were tested against 16,000 ppm and 20,000 ppm NaCl. These levels were found to be critical for barley seeds at germination. The salt solutions were prepared by dissolving an equivalent amount of table salt (Iodine free) in a proper volume of distilled water.

Twenty-five seeds from each variety were placed in a 15 x 1.7 cm test tube. A volume of 15 cc of solution was poured into the test tubes. The test tubes were then placed in the growth chamber at 12°C for 48 hours. The solutions were changed every 12 hours.

At the end of 48 hours, the solutions were filtered off and the kernels mopped to remove excess moisture. They were then placed back in their test tubes and stoppered with porous foam rubber. The test tubes were placed in the growth chamber at 17°C for 6 days. On alternate days the germinating seeds were carefully removed from the test tubes, to prevent rootlets from tangling together. This test was repeated three times.

II. Mature-Plant Test:

This test was made to determine the degree of tolerance of barley plants during later growth stages. The same varieties of barley mentioned in the germination test were used. The seeds were taken from plants grown the previous season.

Plants were grown in pots, using sandy loam soil. California Mariout, a known salt tolerant variety, was used as a check variety. Two seeds of each variety along with two seeds of California Mariout were planted in each pot. Three concentrations of sodium chloride (iodine free table salt) were used, 0, 16,000 and 24,000 parts per million. A total of 15 pots per replication were employed and the experiment was replicated three times. Pots as well as replications were randomly distributed and placed on three individual benches. The benches were about 30 cm high and wide enough to leave space among pots for better illumination.

The experiment was conducted in the growth chamber, where the temperature was kept at 18°C during day hours and 10°C during night hours. A total of 16 hours of light were received by the plants daily.

Seeds were sown on April 30, 1978. Treatment solutions were applied on the 14th of May when the plants were in the three to four leaf stage. Each culture was to receive about one third of a liter of the solution on an alternate day. On the other days, the cultures were flooded with water to prevent salt accumulation. A complete fertilizer was applied to the plants once a week. Pots were rotated every week within and between replications.

On the 28th of July, 1978, plants were harvested for measurements. The harvesting was done at the soil surface so that only the upper portions of the plants were involved in the readings. Fresh weight, height, tiller number, and the dry weight of the plants were taken. Measurements on plant roots were ignored due to the difficulties in obtaining the roots of each individual plant. Yield was also ignored since the varieties had different maturity dates.

III. Diallel Cross:

To study the inheritance of salt tolerance in barley plants during the germination stage, a 6 x 6 diallel cross was made. Diallel cross analysis by Jinks (37) and Hayman (33) was employed in this study since salt tolerance was found to be a continuous rather than discrete variable (41).

All possible crosses, including selfing between the selected parents were made with the assumption 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 (Vp)
2) the variance of the offspring of each parental

array (Vr) and,

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

The regression of Wr and Vr was obtained and Vr was plotted against Wr. Consistency of (Wr - Vr) over arrays and the significance of the regression of Wr on Vr should jointly indicate the validity of the hypothesis postulated. Consistency of (Wr - Vr) was tested by using the formula:

$$t = \sqrt{\frac{r-2}{4}\ (\text{Var Vr} - \text{Var Wr})^2/\text{Var Vr} \times \text{Var Wr} - \text{cov}^2(\text{Vr},\text{Wr})}$$

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 Wr on Vr 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 $S_b = \sqrt{S^2y.x/\Sigma X^2}$ 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 $Wr^2 = Vp\ Vr$, delimited the area in which coordinate data (Wr, Vr) 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.

The diallel cross was made among six parental varieties mentioned earlier in this chapter. The fifteen crosses of the 6 x 6 diallel were made in the greenhouse in the winter of 1977. F_1 seeds were grown in the greenhouse to obtain F_2 seeds. F_2 seeds were then grown in the field to obtain F_3 seeds. The study material was confined to the F_3 seeds of the 15 crosses due to the low amount of F_2 seeds. The F_3 seeds of the 15 crosses along with the six parents were tested for salt tolerance at the germination stage in a 16,000 ppm NaCl solution as described earlier.

RESULTS

1. Mature plant test:

These results indicate that the salt concentration gradient had a depressing effect on the dry weight of the six varieties studied. Increasing salt concentrations significantly reduced the growth of the plants as represented by the dry weight (Figure 1).

The regression analysis in Figure 1 indicates a strong linear relationship between dry weight and salt concentration. The analysis of variance (Table 2) for the dry weight and the regression analysis show significant differences between the six varieties.

TABLE 2. Mean squares of salt tolerance scores as represented by dry weights of the six varieties of barley at maturity.

Source of Variation	Degrees of Freedom	Mean Square	F
Blocks	2	25.963	
Entries	5	100.788	7.185**
Error (a)	10	14.028	
Treatment	2	1202.884	118.69**
Entries x treatment	10	35.236	3.477**
Error (b)	24	10.134	

** $P \leq 0.01$

The regression lines in Figure 2 show that there are two kinds of behavior: varieties Orge Saida 183, Coho, and California Mariout have a similar performance and may be considered salt tolerant, while other varieties showed sensitivity to salt.

Differences between regression lines of the six varieties showed different levels of significance. A significant difference ($p < .05$) was found between Lajbjey Drosihezy A and Orge Saida 183, California Mariout, and Coho (Table 3). There were no significant differences among the last three varieties.

Regression lines of the varieties Lajbjey Drosihezy A, Ingrid, and Mashu Mugi show different patterns, but all have greater negative response when compared to the rest. Lajbjey Drosihezy A seems to be the most affected by salt concentration. Ingrid and Mashu Mugi show similar reactions to salt.

Fresh weight has also shown a strong linear relationship with salt concentration (Figure 3). Differences between regression means were not significant, although regression lines of the six varieties show somewhat different patterns (Figure 4). Varieties Ingrid and Mashu Mugi appear to be more depressed than the others. Lajbjey Drosihezy A lies close to Orge Saida 183, Coho, and

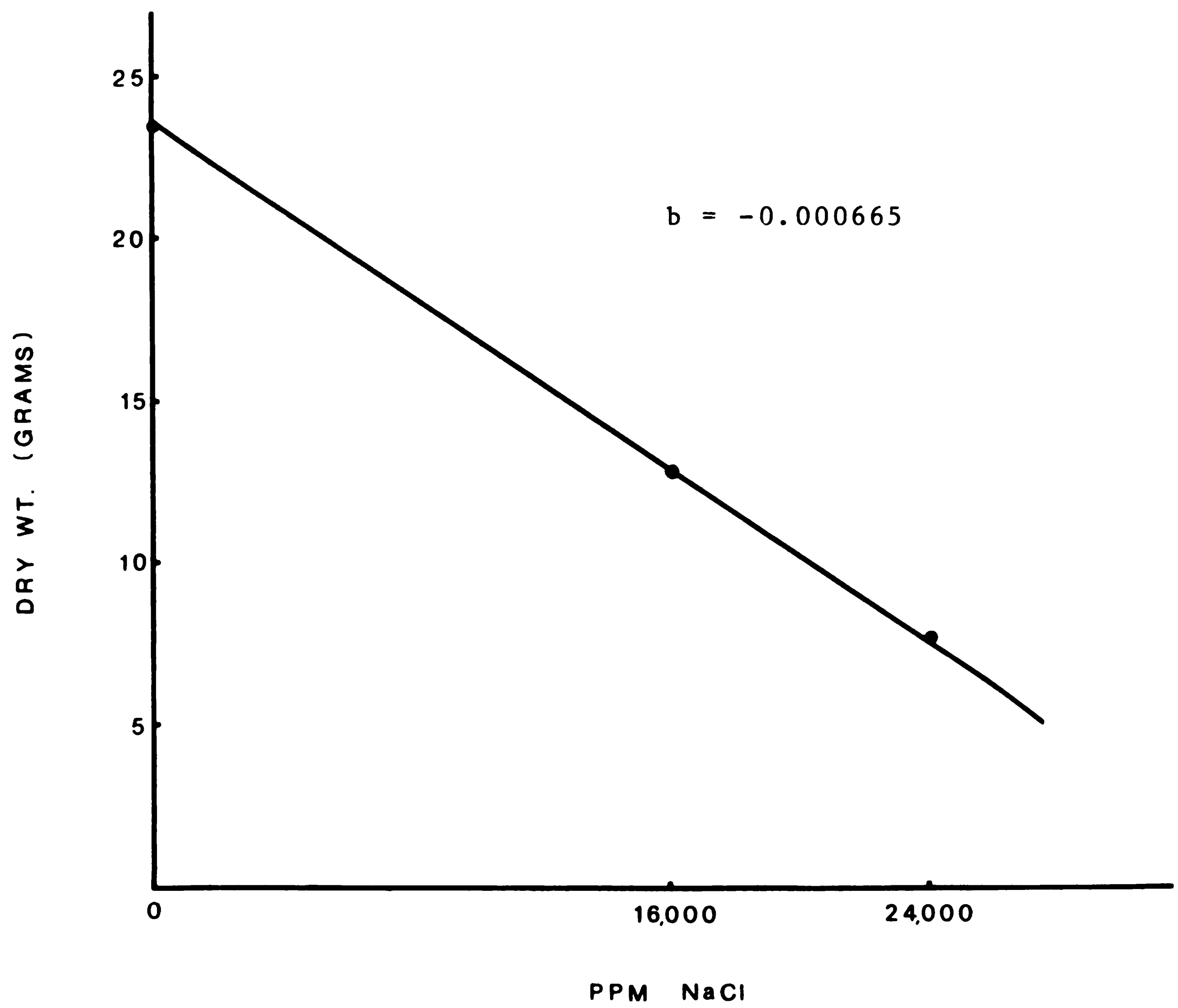

FIG. 1 - Effect of NaCl concentration on the total dry weight of 6 barley varieties.

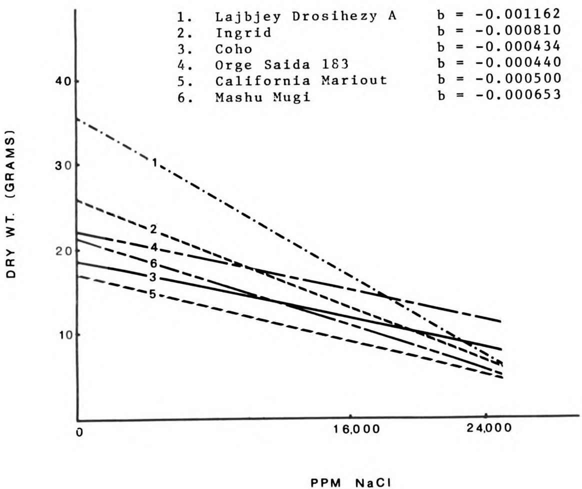

FIG. 2 - Effect of NaCl concentration on the dry weight of 6 barley varieties.

TABLE 3. t values for the difference between two slopes for the six varieties of barley for dry weight, fresh weight, height and tiller number.

Varieties	Dry Weight	Fresh Weight	Height	Tiller Number
L. Drosihezy A and				
Ingrid	2.958†	0.33	0.27	1.106
Coho	6.12**	0.245	0.79	3.247*
O. Saida 183	6.068**	0.39	0.94	3.558*
C. Mariout	5.564**	0.22	0.682	2.09
Mashu Mugi	4.278*	0.49	0.02	2.58
Ingrid and				
Coho	3.16*	0.57	0.79	2.14
O. Saida 183	3.12*	0.723	1.2	2.45
C. Mariout	2.6	0.111	0.952	0.98
Mashu Mugi	1.32	0.1629	0.29	1.476
Coho and				
O. Saida 183	0.05	0.148	0.146	0.312
C. Mariout	0.5	0.46	0.109	1.156
Mashu Mugi	1.84	0.74	0.77	0.664
O. Saida 183 and				
C. Mariout	0.5	0.65	0.256	1.467
Mashu Mugi	1.79	0.923	0.92	0.97
C. Mariout and				
Mashu Mugi	1.29	0.274	.663	0.492

† $P \leq 0.10$ * $P \leq 0.05$ ** $P \leq 0.01$

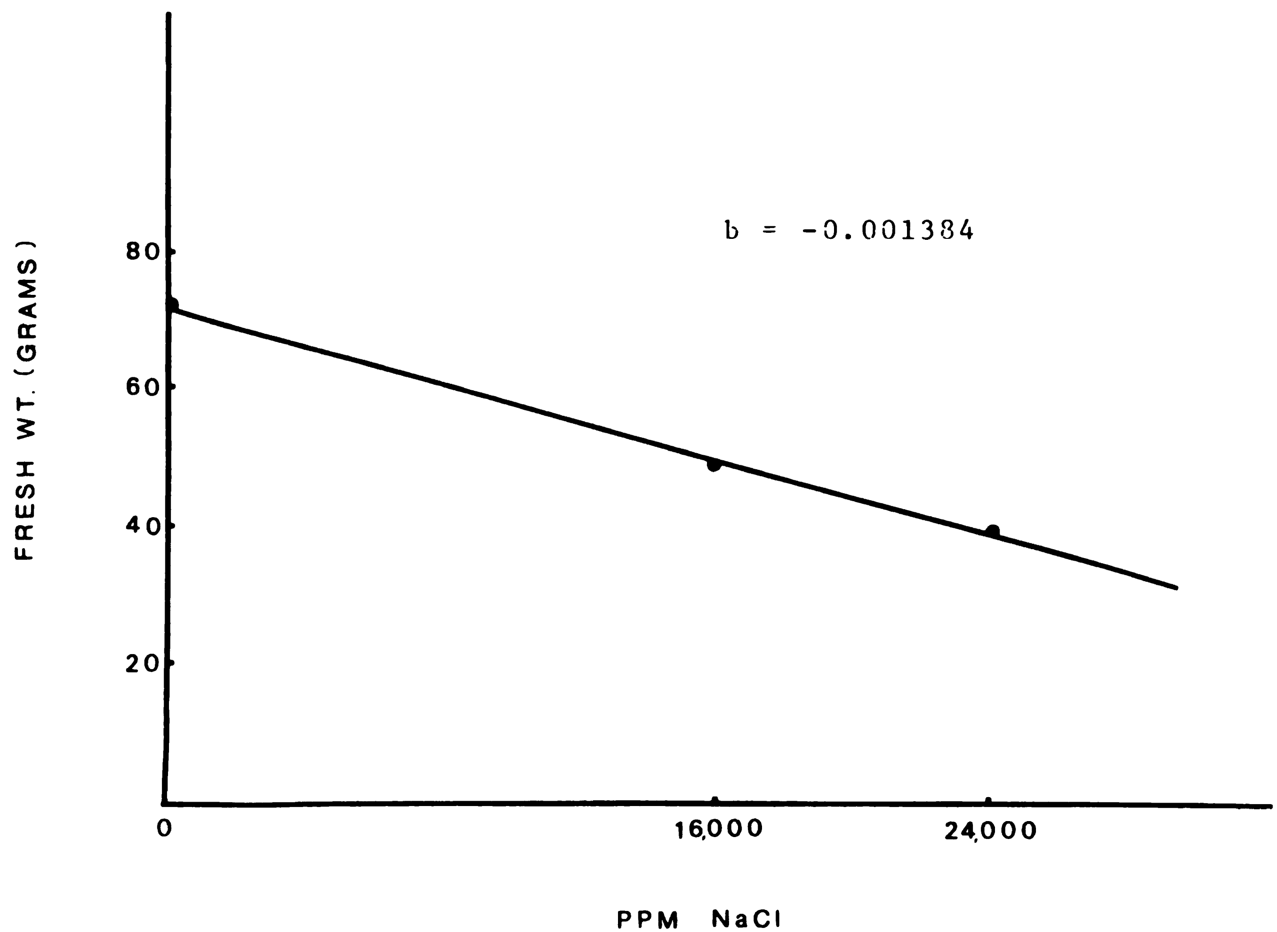

FIG. 3 - Effect of NaCl concentration on the total fresh weight of 6 barley varieties.

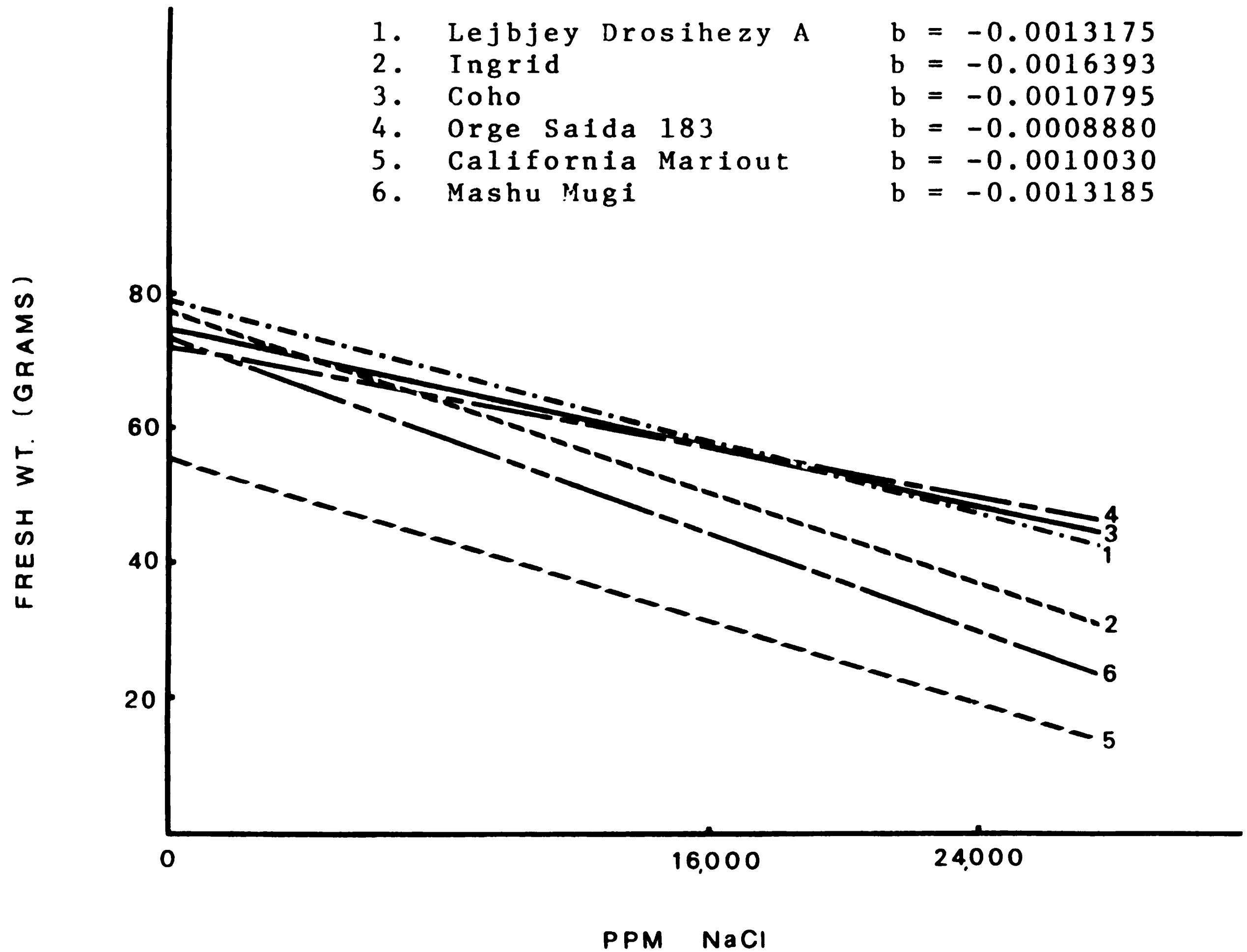

FIG. 4 - Effect of NaCl concentration on the fresh weight of 6 barley varieties.

California Mariout in terms of their regressions. The analysis of variance is summarized in Table 4.

TABLE 4. Mean squares of salt tolerance scores as represented by fresh weights of the six varieties of barley at maturity.

Source of Variation	Degrees of Freedom	Mean Square	F
Blocks	2	105.951	
Entries	5	1137.813	41.86**
Error (a)	10	27.182	
Treatment	2	6378.513	109.1943**
Entries x treatment	10	112.472	1.925†
Error (b)	24	58.414	

† $P \leq 0.10$ ** $P \leq 0.01$

Height of the six varieties also decreased as a function of salt concentration as shown in the strong linear relationship (Figure 5). No significant differences between regressions were found (Table 3). Regression lines of the varieties Orge Saida 183, Coho, and California Mariout have a similar behavior as shown in Figure 6. Heights of Ingrid, Mashu Mugi and Lajbjey Drosihezy A, were regressed in a similar manner, but showed more depression than the first group.

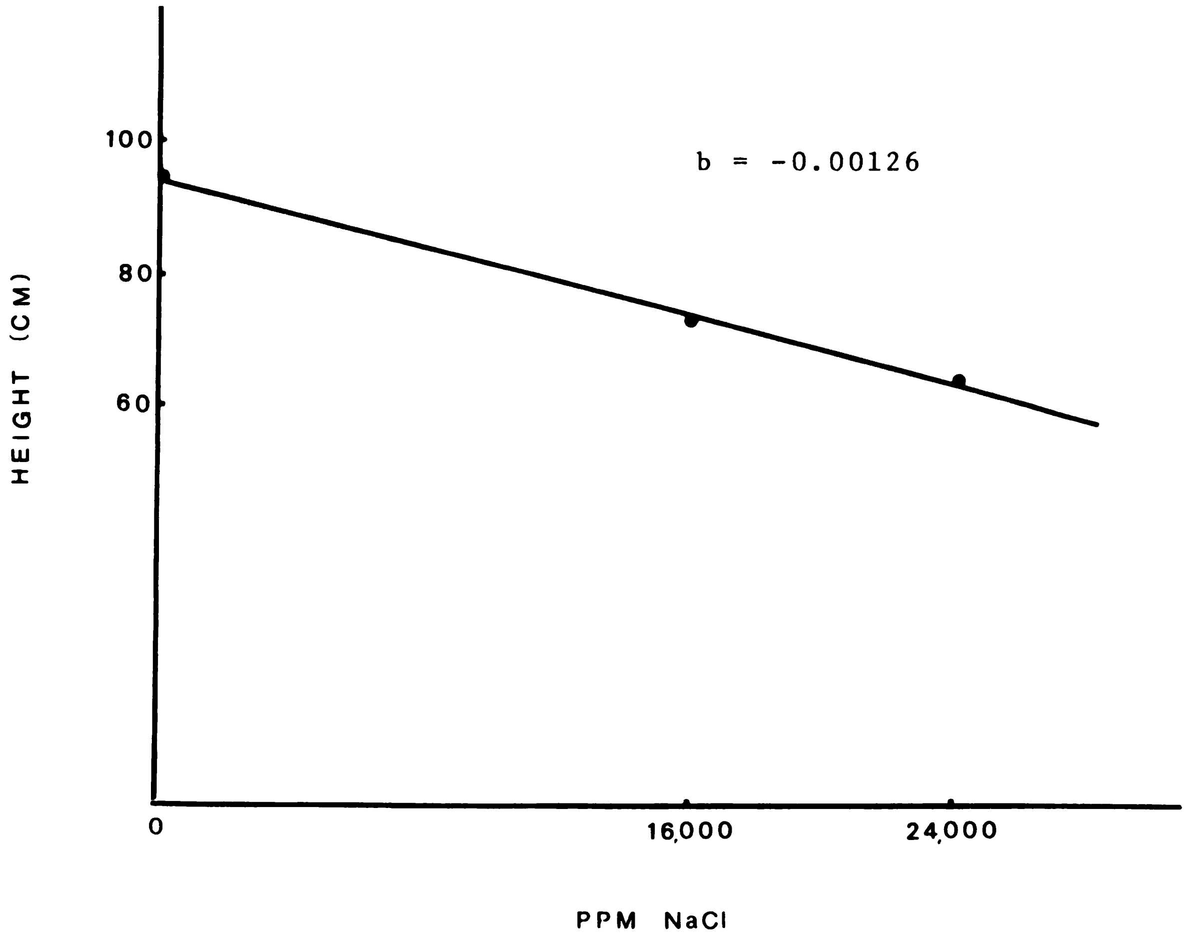

FIG. 5 - Effect of NaCl concentration on the total height of 6 barley varieties.

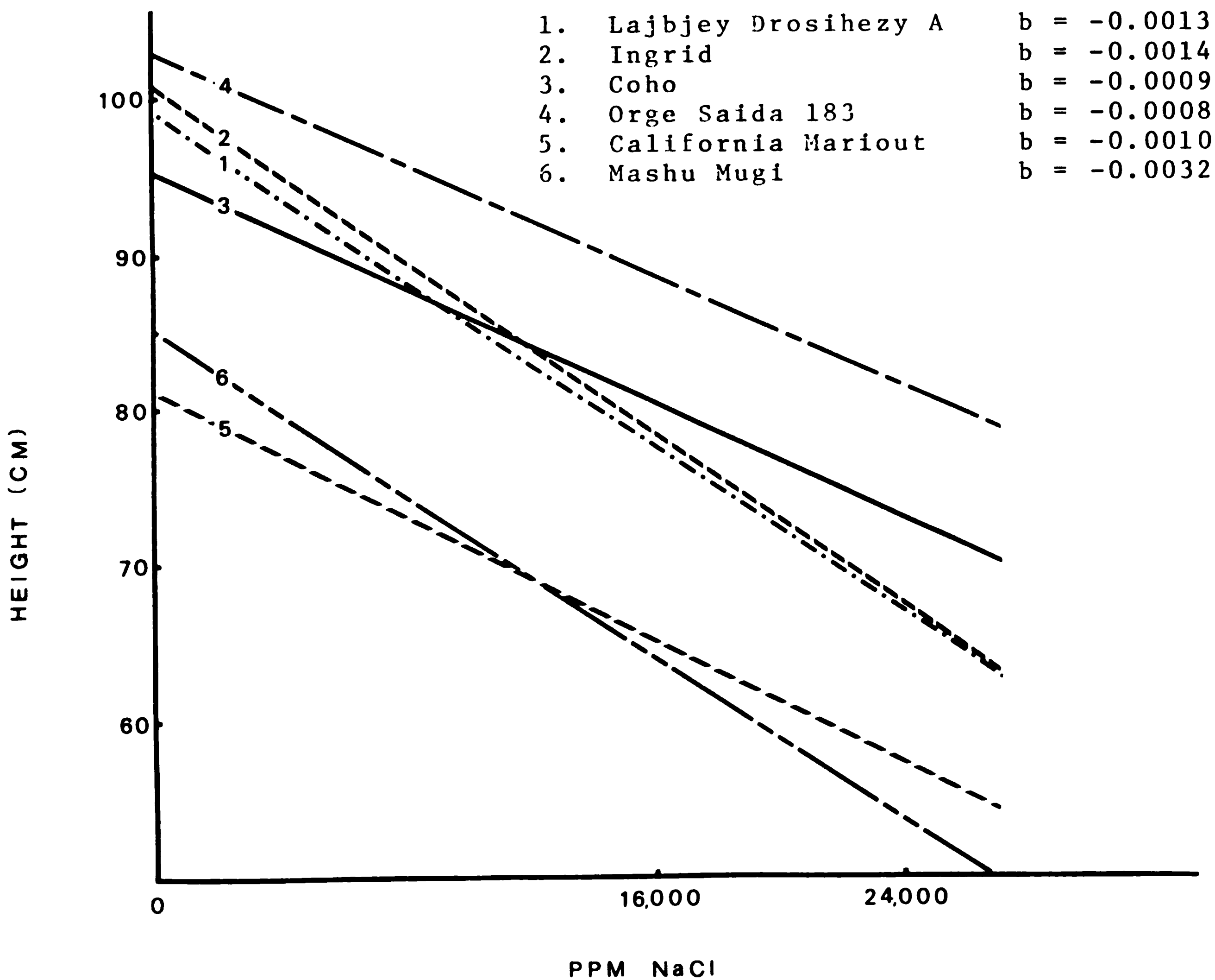

FIG. 6 - Effect of NaCl concentration on the height of 6 barley varieties.

The analysis of variance (Table 5), however, showed no significant differences regarding the entry-treatment interactions.

TABLE 5. Mean squares of salt tolerance scores as represented by heights of the six varieties of barley at maturity.

Source of Variation	Degrees of Freedom	Mean Square	F
Block	2	32.932	
Entries	5	502.833	15.0677**
Error (a)	10	33.372	
Treatment	2	3807.315	67.11**
Entries x treatment	10	44.288	.781
Error (b)	24	56.736	

** $P \leq 0.01$

A strong linear relationship between tiller number and salt concentration was also found (Figure 7). Figure 8 shows the effect of salt concentration on tiller number of the six varieties. Orge Saida 183 and Coho show superior performance under even the highest concentration (24,000 ppm). California Mariout and Mashu Mugi show some depression, while Lajbjey Drosihezy A and Ingrid were the most affected

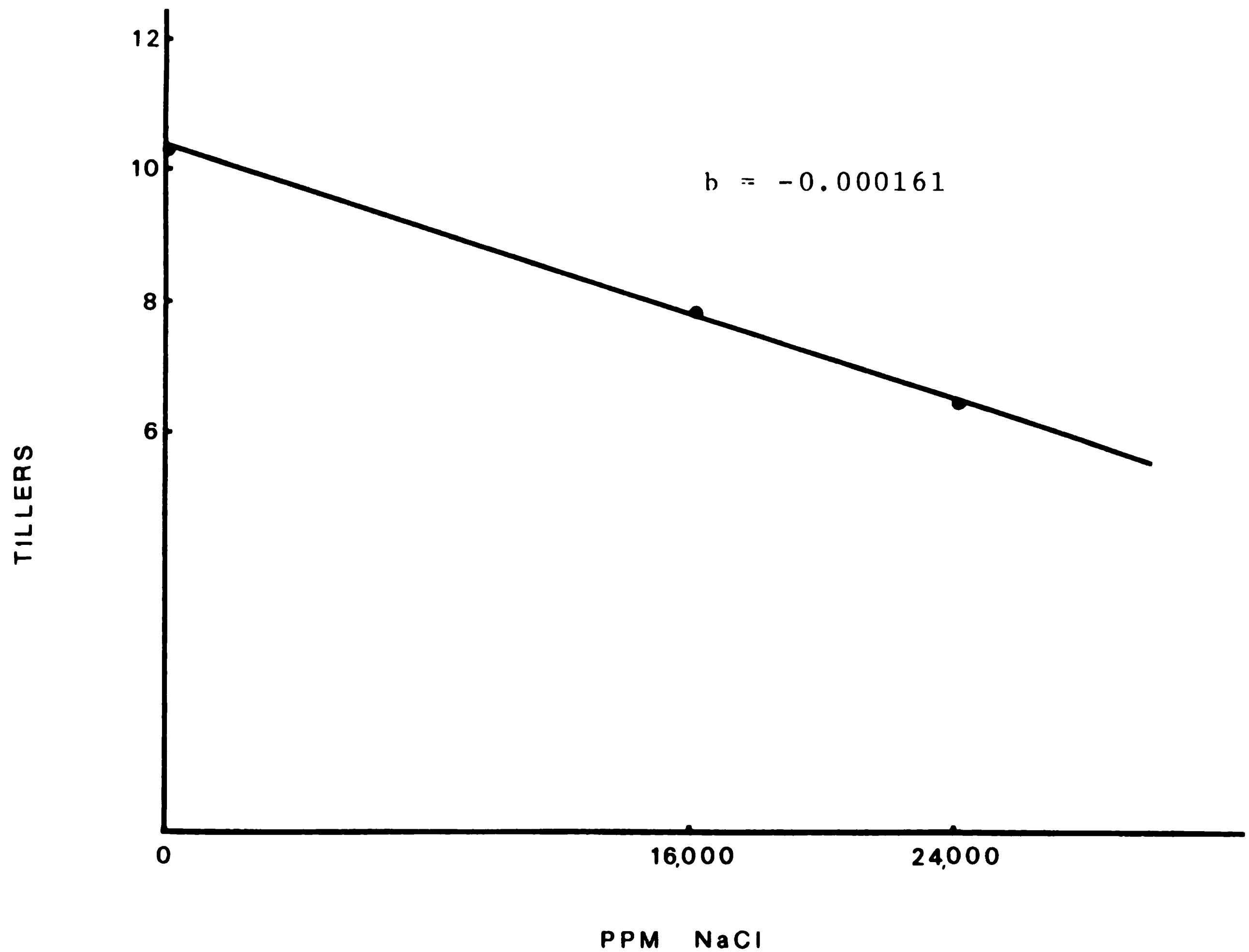

FIG. 7 - Effect of NaCl concentration on the total tiller number of 6 barley varieties.

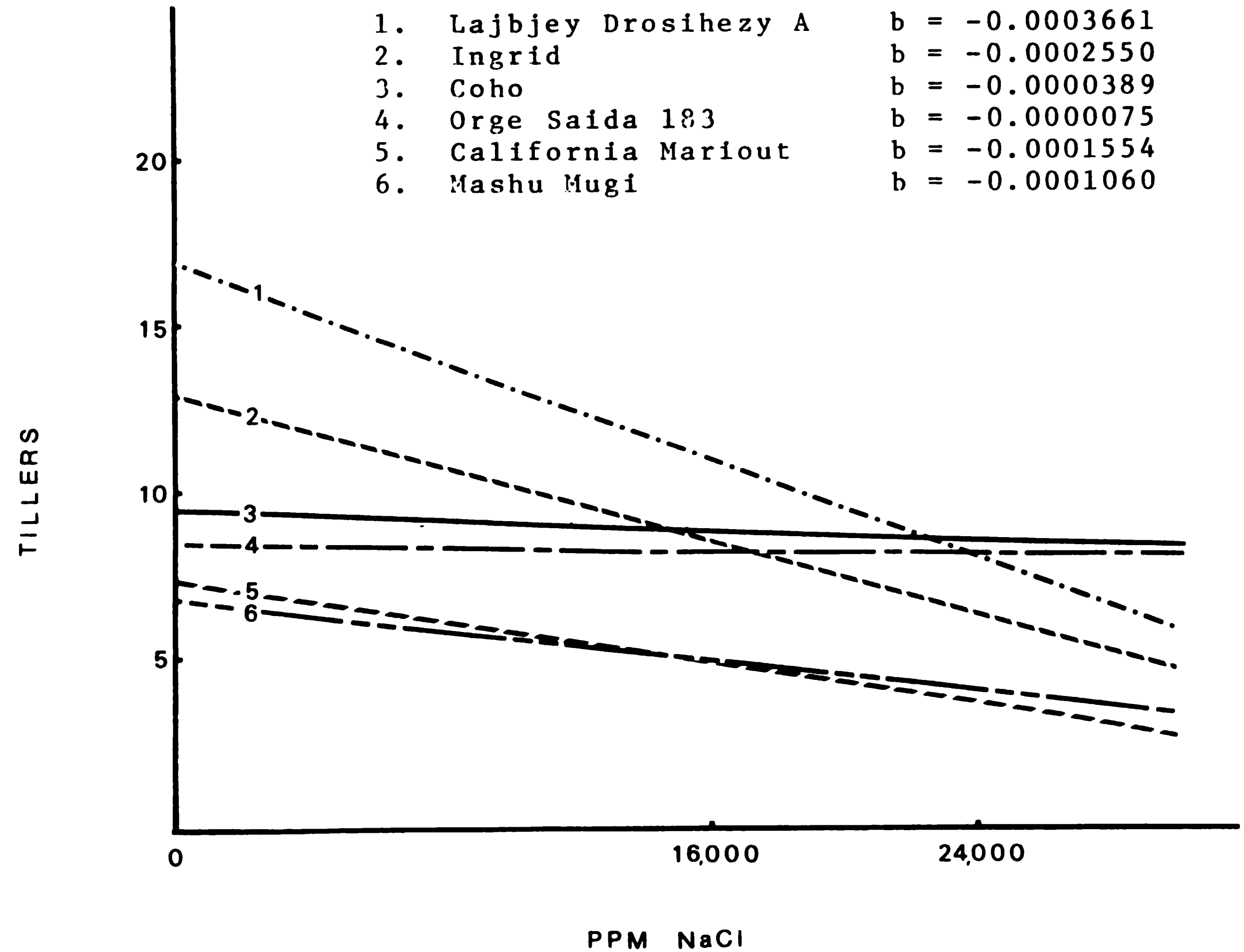

FIG. 8 - Effect of NaCl concentration on the tiller number of 6 barley varieties.

by salt concentration. The analysis of variance is summarized in Table 6.

TABLE 6. Mean squares of salt tolerance scores as represented by tiller number of the six varieties of barley at maturity.

Source of Variation	Degrees of Freedom	Mean Square	F
Block	2	2.905	
Entries	5	58.716	24.98**
Error (a)	10	2.350	
Treatment	2	66.812	15.15**
Entries x treatment	10	8.156	1.849
Error (b)	24	4.410	

** $P \leq 0.01$

The average moisture content (grams) per gram of dry matter of the above ground parts for the six varieties at the three concentrations was calculated and shown in Table 7. Generally, the six varieties had more moisture per gram of dry matter in the 16,000 and 24,000 ppm than in the control, except for California Mariout which did the reverse. Lajbjey Drosihezy A, seems to have more moisture per gram of dry matter at the 16,000 ppm and the 24,000 ppm than did the rest. Ingrid and Mashu Mugi have shown a moderate accumulation of moisture in their tissues. Coho and Orge Saida 183 have shown the least moisture per gram of dry matter. California Mariout absorbed less water per gram of dry matter in both the 16,000 and the 24,000 ppm than did the control.

TABLE 7. Average moisture content (grams) per gram of dry matter of the six varieties of barley at three levels of salinity.

Variety		NaCl Concentration	
	0 ppm	16,000 ppm	24,000 ppm
1. Lajbjey Drosihezy A	1.12	3.10	4.19
2. Ingrid	1.85	3.45	3.24
3. Coho	2.88	4.08	4.64
4. Orge Saida 183	2.14	3.00	3.05
5. California Mariout	2.16	1.85	1.89
6. Mashu Mugi	2.33	3.09	4.10

The varieties Lajbjey Drosihezy A and Mashu Mugi show a proportional relationship between moisture content and salt concentration, i.e. moisture content increased as a function of increasing salt concentration. This is not true, however, for the rest of the varieties since they retained moisture at a similar level in the 16,000 and the 24,000 ppm.

2. Germination test:

The germination test showed that increasing salt concentration significantly decreased germination percentage of the six varieties of barley tested.

The regression analysis (Figure 9) shows that there is a strong linear relationship between salt concentration and germination percentage. The six varieties of barley behaved differently to salt treatment as shown by their different regression lines (Figure 10) and the analysis of variance (Table 8). California Mariout was superior when

TABLE 8. Mean squares of salt tolerance scores as represented by germinating seeds of the six varieties of barley.

Source of Variation	Degrees of Freedom	Mean Square	F
Block	2	1.241	
Entries	5	119.529	23.91**
Error (a)	10	2.085	
Treatment	2	1203.574	309.5**
Entries x treatment	10	25.619	6.5879**
Error (b)	24	3.889	

** $P \leq 0.01$

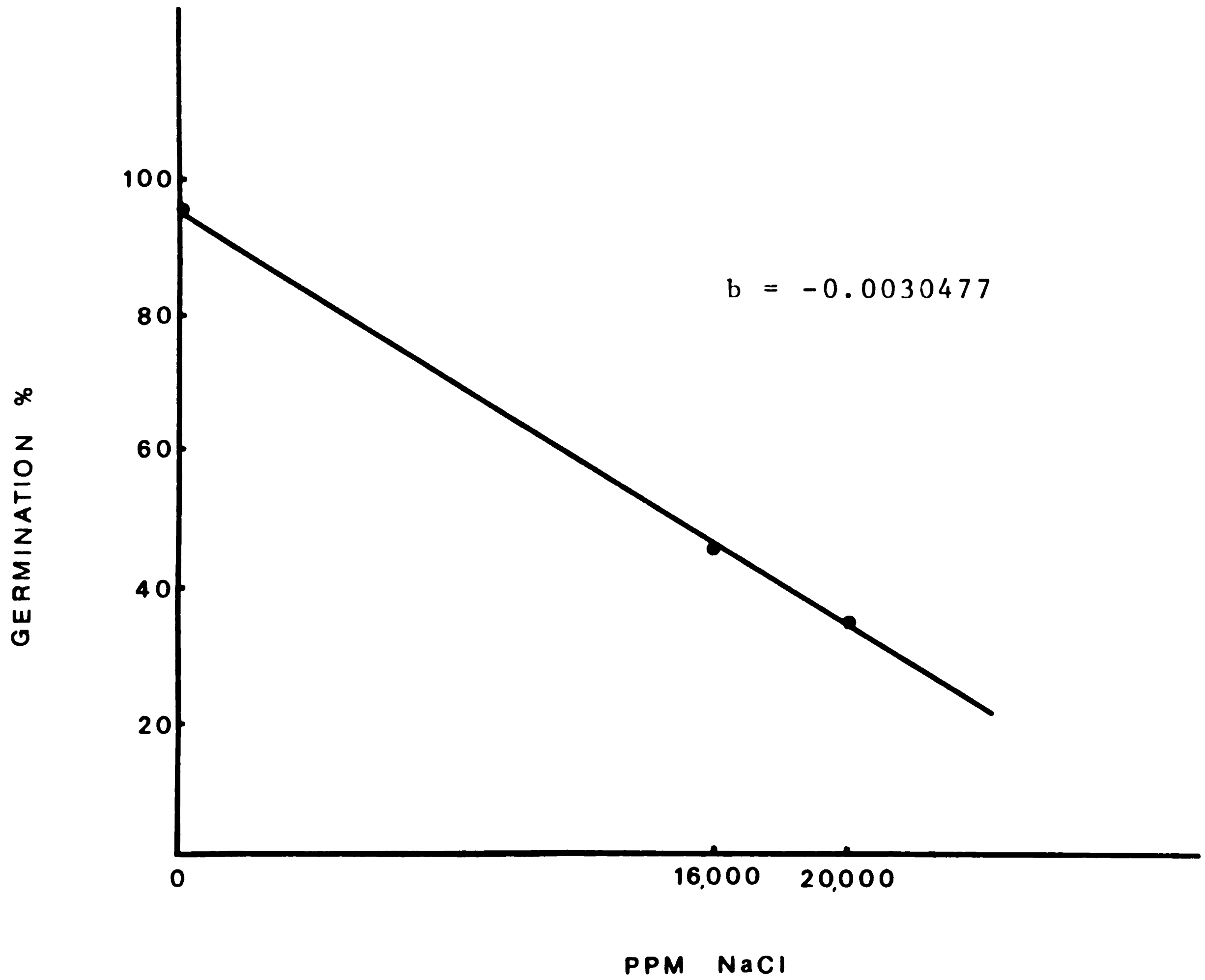

FIG. 9 - Effect of NaCl concentration on the total germination percentage of 6 barley varieties.

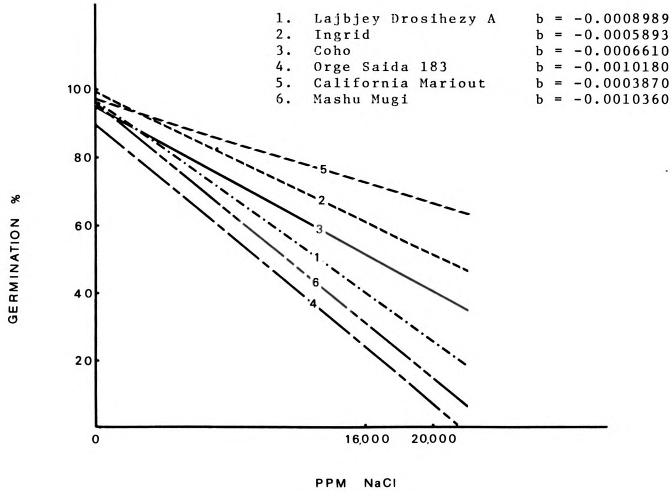

FIG. 10 - Effect of NaCl concentration on the germination percentage of 6 barley varieties.

compared to other varieties. Varieties Lajbjey Drosihezy A, Orge Saida 183, and Mashu Mugi were most affected by salt, while varieties Ingrid and Coho have shown an intermediate performance. According to their performance in the germination test, California Mariout was considered salt tolerant; Ingrid and Coho were intermediate; Lajbjey Drosihezy A, Orge Saida 183, and Mashu Mugi salt sensitive.

Differences among regression lines were calculated and showed different degrees of significance (Table 9). Highly significant differences were found between California Mariout and the salt sensitive varieties; while significant differences were found between the later lines and the intermediate ones. No significant differences, however, were shown between California Mariout and the intermediate lines.

Correlations between tolerance to salt during the germination stage and the mature-plant stage were calculated (Table 10). The regression coefficients obtained for the six lines in the germination stage were correlated with those of dry weight, fresh weight, height, and tiller number in the mature-plant stage. The regression coefficients were used in this test because they represent an estimate for tolerance to salt.

TABLE 9. t values for the difference between two slopes for the six varieties of barley for germination.

Varieties	t
Lajbjey Drosihezy A and	
Ingrid	1.59
Coho	1.22
Orge Saida 183	.612
California Mariout	2.63†
Mashu Mugi	.7
Ingrid and	
Coho	.37
Orge Saida 183	2.2†
California Mariout	1.04
Mashu Mugi	2.3†
Coho and	
Orge Saida 183	1.83
California Mariout	1.41
Mashu Mugi	1.93
Orge Saida 183 and	
California Mariout	3.24*
Mashu Mugi	.093
California Mariout and	
Mashu Mugi	3.34*

† $P \leq 0.10$ * $P \leq 0.05$

TABLE 10. The correlations among regression coefficients for germination % and mature-plant characteristics.

Stage of Growth	d.f.	r
Germination and dry weight	4	+ .183
Germination and fresh weight	4	- .061
Germination and height	4	+ .371
Germination and tiller number	4	- .158

The calculated r values for germination and dry weight and germination and height were positive while they were negative for fresh weight and tillers. These values, however, were not found significant, indicating no significant correlation between salt tolerance in the two stages of growth.

3. Genetic investigation:

The genetic investigation will be discussed on the basis of the results of the salt tolerance tests in the germination stage on the F_3 progenies of the 6 x 6 diallel set. The diallel cross data is required to show a significant variation among hybrids for the test to contain reliable genetic information. The step is usually examined prior to carrying on further analysis.

The results of the analysis of variance of the fifteen F_3 hybrid progenies for salt tolerance test at the germination stage is presented in Table 11. A highly significant

TABLE 11. Mean squares for salt tolerance scores in the germination stage of the F_3 of the 6 x 6 diallel cross set.

Source of Variation	Degrees of Freedom	Mean Square	F
Block	2	11.822	
Entries	14	47.876	6.353**
Error (a)	28	7.537	
Treatment	2	3817.356	655.9**
Entries x treatment	28	13.998	2.41**
Error (b)	60	5.820	

** $P \leq 0.01$

difference existed among entries. Consequently, the genetic relationship among this set of selected parents and progenies was analyzed using the technique of the Jinks-Hayman diallel cross analysis and the graphical analyses were based on the variance and the covariance of the arrays.

The F_3 data of salt tolerance in the germination stage is summarized in Table 12. Each value is the average germination percentage of 75 F_3 seeds. The array's variance

(Vr) and covariance (Wr) are shown on the right hand side of the table.

The table shows that the means of the crosses do not consistently lie in the range of the parents. Crosses 1 x 2, 2 x 4, 2 x 6, 3 x 4, 3 x 6, 4 x 5, and 5 x 6 have a mean value in the range of their parents. Cross 1 x 6 was the only combination that showed transgressive effect since the mean was higher than the mean of either of its parents. The mean values of crosses 1 x 3, 1 x 5, 2 x 3, 4 x 6 were close to that of parents 3, 1, 2, and 4, respectively. Crosses that showed mean values less than their lower parents were 1 x 4, 2 x 5, and 3 x 5. The Vr values show that array 3 was the least variable and array 5 the most variable.

The t values for the test of the consistency of the variable (Wr - Vr) over arrays was calculated at t = 1.66 and found to be not significant (P > .90) indicating the validity of the postulated hypothesis. The regression graph of Wr on Vr is shown in Figure 12 along with the limiting parabola $Wr^2 = WpVr$.

The graphical analysis shows that Wr and Vr enjoy an almost linear relationship with the regression coefficient b = 1.533** significantly greater than zero but not more than one.

TABLE 12. Average germination percentages of the F_3 of the 6 x 6 diallel cross set.

Parental Number	Parents	1	2	3	4	5	6	Vr	Wr
1	L. Drosihezy A	44.00						248.772	213.400
2	Ingrid	56.00	69.33					222.157	160.561
3	Coho	62.67	72.00	61.33				109.841	35.391
4	O. Saida 183	17.33	32.00	56.00	21.33			202.992	116.898
5	C. Mariout	44.00	49.33	45.00	30.67	78.67		258.619	294.635
6	Mashu Mugi	52.00	64.00	45.33	20.00	42.67	34.67	225.170	230.987

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

The graph shows that the most tolerant variety, parent 5 is located at the recessive side of the regression graph, and parent 3 a moderately tolerant variety at the dominant side of the graph. This means that parent 3 carries most of the dominant genes and parent 5 carries most of the recessive alleles present in this sample of parents. Parent 5 is the most tolerant variety and parent 3 is moderately tolerant to salt at the germination stage. This suggests the possibility of having at least two sets of genes governing salt tolerance.

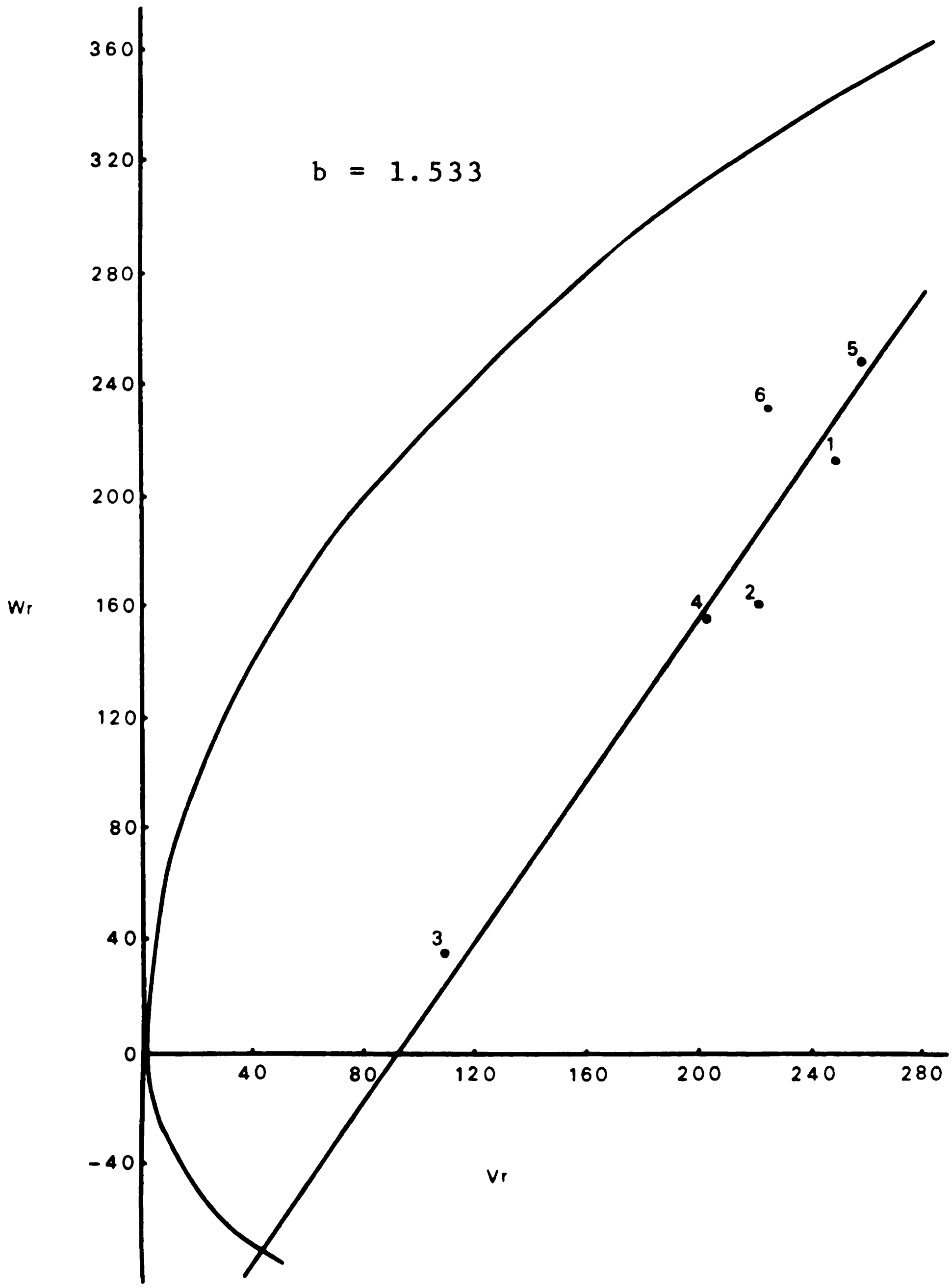

FIG. 11 - Wr/Vr graph analysis of germination percentage of the F_3 of the 6 x 6 diallel cross set.

DISCUSSION

This study consists of three phases. First, I endeavored to show the effect of salt on germination and second, to show the effect of salt on the mature plants. The two do not appear to be correlated, leading one to hypothesize the existence of at least two different sets of genes governing resistance. The third phase of this study involves the inheritance of resistance to salt in the germination stage.

The regression coefficients (b values) were used to detect varietal differences. According to these values, the mature-plant test showed obvious varietal differences for fresh weight, dry weight, height, and tiller number. Varieties Orge Saida 183, Coho, and California Mariout showed less reduction in the fresh weight, dry weight, and height under saline conditions than the other varieties. As for tiller number, varieties Orge Saida 183 and Coho showed superior performance as they maintained a high tiller number in the two levels of NaCl. California Mariout, however, produced a lesser number of tillers per plant as it showed smaller b value (-0.00015540) than Orge Saida 183 (b = -0.00000750) and Coho (b = -0.00003893).

Based on the b values for the dry weight and height, California Mariout, Orge Saida 183, and Coho can be considered salt tolerant, as they showed b values of -0.000500,

-0.000440, and -0.000434 for the dry weight, and -0.0010000, -0.0008800, and -0.0009510 for height. Lajbjey Drosihezy A, Ingrid, and Mashu Mugi were salt sensitive during the mature plant stage. Their b values were -0.001162, -0.000810, and -0.000653 for the dry weight, and -0.0013275, -0.0014560, and -0.0032000 for height.

The data on moisture content under saline conditions revealed that barley plants accumulate more water per gram of dry matter (Table 7) under high salt conditions with the exception of California Mariout. These results disagree with those obtained by Eaton (26) in which he found that water requirements of wheat and saltbush decreased as salinity increased. The results from the present study, however, coincide with Eaton's later results (27) in which water requirements for mixed culture of eight crops increased at higher levels of salinity. This increase of water may have been due to the accumulation of additional salt in plant tissue.

The data showed that tolerant varieties represented by California Mariout, Orge Saida 183, and Coho accumulated less water per gram of dry matter as compared to the sensitive ones (Table 7). This may suggest that tolerant varieties accumulated less salt in their tissue. This, however, is not definite due to the lack of supportive data.

It is interesting to notice that California Mariout, a well known tolerant variety, maintained a low moisture content at all levels of salinity. According to Scholander et al. (47) and Atkinson et al. (6) in explaining their theories of excluding or excreting the salt by the roots or through special glands on the leaves, one might classify California Mariout as either a good excluder or good excreter.

Germination tests revealed that the most tolerant variety was California Mariout, while Ingrid and Coho were rated intermediate and Lajbjey Drosihezy A, Orge Saida 183, and Mashu Mugi were considered sensitive to salt at that stage as indicated by their b values. The b values were -0.00038700, -0.0005893, -0.00066100, -0.00089893, -0.00101800, and -0.00103600 for California Mariout, Ingrid, Coho, Lajbjey Drosihezy A, Orge Saida 183, and Mashu Mugi respectively. This agrees with Maddur's (41) classification except for the variety Lajbjey Drosihezy A, which he considered salt tolerant. Although a similar method was used in this study, measurements were taken on different characters. In this study, germination percentage was used to determine tolerance to salt, while coleoptile length was utilized in the other study.

Results from the germination test and the mature-plant test show that tolerance to salt is not consistent throughout the life cycle of barley plants. Varieties Lajbjey Drosihezy A and Mashu Mugi show sensitivity to salt during both stages of growth. Orge Saida 183, a sensitive variety during the germination stage was considered tolerant to salt during the mature-plant stage. Ingrid and Coho had an intermediate tolerance to salt at germination, but yet behaved differently during the mature-plant stage; as the first variety showed sensitivity and the second tolerance to salt. The only variety that coped very well with salt in both stages was California Mariout. These results agree with those obtained by Norlyn, et al. (43). They found that barley cultivars showed different responses throughout their life cycle.

No significant correlation of salt tolerance between the germination stage and mature-plant stage was found (Table 10). This might suggest the presence of a least two sets of genes controlling tolerance to salt at the two stages of growth.

The graphical analysis of the germination stage test (Figure 11) showed that parent 3 with an intermediate tolerance to salt is located at the dominant side of the Wr/Vr regression graph and parent 5, the most tolerant variety at the recessive side. Thus, the F_3 progenies of parent 3 (Coho) have the least variance (Vr) and covariance

(Wr), and parent 5 (California Mariout) has the highest (Vr) and (Wr). By examining the salt tolerance scores of the progenies of this parent with other parents, we see that it has a low combining ability. This is a case which neither Jins (37) nor Hayman (33) discussed in their theory, probably because it is not likely to occur. The reason for this discrepancy could be related to the differences in origin. California Mariout originated in Egypt, Coho in the USA, Ingrid in Sweden, Lajbjey Drosihezy A in Denmark, Mashu Mugi in Japan, and Orge Saida 183 in Algeria. Although the last parent originated near Egypt, it's progenies with California Mariout showed scores similar to it. Orge Saida 183, however, was found sensitive to salt at the germination stage.

It is important to mention that we are dealing with F_3 populations in which the frequency of the heterozygotes under selfing has been reduced to 25% in contrast to 100% in the F_1 populations. In effect, dominance is expected to decrease in the F_3 populations. This, however, is best represented by a considerable but not significant increase in the b value from 1 to 1.533 (Figure 11). Along with changing the slope, the regression line has also been shifted to the right. This is caused by an increase in the total genetic variance among the F_3 populations.

As indicated earlier that parent 3 possesses most of the dominant genes which resulted from having the least Vr and Wr. On the other hand, parent 1, representing the variety Lajbjey Drosihezy A possesses most of the recessive alleles due to having the highest Vr and Wr, with the exception of California Mariout. Since parent 3 (Coho) possesses a considerable tolerance to salt (b = -0.0006610) and parent 1 (Lajbjey Drosihezy A) is sensitive to salt (b = -0.00089893), one might suggest that tolerance to salt in all varieties but California Mariout at the germination stage is controlled by dominant genes (Figure 11).

As for California Mariout, two points should be considered. Firstly, it is well known that it possesses an outstanding tolerance to salt in the germination stage (9, 31, 41). According to Maddur's findings (41), tolerance to salt at that stage is controlled by dominant genes. One would then assume that California Mariout should be at the dominant side of the graph (Figure 11) and not at the recessive side as this study concluded. Secondly, this variety showed consistency when crossed with other parents. These results lead to speculation that California Mariout possesses a different genetic system for salt tolerance than the other varieties. That is, salt tolerance in

California Mariout at the germination stage is controlled by recessive genes.

SUMMARY AND CONCLUSIONS

This study revealed information about the effect of salt on six barley varieties during germination and mature-plant stages. It also acquired information on the genetic basis of salt tolerance in barley during germination stage.

Varietal differences for tolerance to salt were obvious during germination stage and mature-plant stage. Measurements were taken on germination percentage at the germination stage; fresh weight, dry weight, height, and tiller number at the mature-plant stage.

California Mariout, a variety originated in Egypt, was the only variety that showed tolerance to salt during both stages of growth. Lajbjey Drosihezy A and Mashu Mugi showed sensitivity at both stages. Orge Saida 183, which was sensitive to salt at the germination stage, showed tolerance to salt in the mature-plant stage. Ingrid and Coho were moderately tolerant to salt at the germination stage, but yet behaved differently during the mature-plant stage; as the first one showed sensitivity and the second one showed tolerance to salt. Tolerance to salt was evaluated according to the regression coefficients obtained for each variety.

No correlation of salt tolerance between germination stage and mature-plant stage was found. There might be at least two sets of genes controlling tolerance to salt at the two stages of growth.

The genetic study involved F_3 populations. It revealed that California Mariout, a known tolerant variety from Egypt, possessed most of the recessive alleles, while Coho, a variety moderately tolerant to salt from USA, possessed most of the dominant genes. The other varieties with various degrees of tolerance to salt possessed different amounts of dominance depending on their locations on the Wr/Vr graph.

The consistency of California Mariout when crossed with other parents led to speculation that it possesses a different genetic system for salt tolerance than the other varieties. That is, salt tolerance in California Mariout at the germination stage is controlled by recessive genes.

As for the rest of the varieties, this study indicated that tolerance to salt at the germination stage is controlled by dominant genes.

The genetic study was done on the F_3 populations in which the frequency of the heterozygotes under selfing had been reduced to 25% in contrast to 100% in the F_1 populations. Dominance was then expected to decrease in the F_3 populations. This, however, was best represented by a considerable but not significant increase in b value from

1 to 1.533. The increase in the total genetic variance among the F_3 populations caused the regression line to shift to the right.

More information is needed on the genetic basis of salt tolerance during other stages of growth.

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