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A QUANTITATIVE ANALYSIS OF PLANT GROWTH

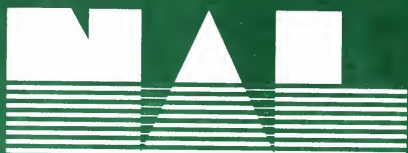
THE EFFECT OF ENVIRONMENTAL STRESSES
ON
FOLIAR EXPANSION OF CASTOR BEANS

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FOREWORD

In presenting the results of this study, recognition must be made of the helpful guidance of the late Dr. Herman E. Hayward who was Director of the U.S. Salinity Laboratory when the greenhouse experimentation was carried out. Appreciation is also expressed to Dr. Hugh G. Gauch, a former colleague at the Salinity Laboratory, who collaborated on a previous work which led to this study and who continued to be an advisor while Professor of Botany at the University of Maryland. The author is especially indebted to Mrs. June B. Walker, laboratory technician, U.S. Regional Salinity Laboratory, who made all the day-to-day observations on plants and environmental conditions during the greenhouse experimentation, and who carefully preserved all records for twenty years until they could be subjected to computer analysis.

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This manuscript should be looked upon as a joint contribution of the U.S. Regional Salinity Laboratory and the U.S.D.A. Hydrograph Laboratory.



A QUANTITATIVE ANALYSIS OF PLANT GROWTH:
The Effect of Environmental Stresses
On Foliar Expansion in Castor Beans

Cecil H. Wadleigh ¹/

The growth responses of any plant are always the integrated effects of prevailing environmental conditions within the genetic limitations of the plant. Much has been learned about the effect of environment on plant response by studies involving specific cultivars in controlled environments wherein all external factors are held constant except the one or two factors having controlled variability. Most plants grow in a natural environment. Continuous variation in external conditions is about the only constant that prevails.

We are deficient in capability to express quantitatively the integration processes prevailing in a plant with respect to external factors as indicated by a given growth response. Naturally occurring stresses may vary widely and become extreme. High or low temperatures, desicating winds, pests, low sunlight, drought, wetness, and a whole array of unamenable soil conditions may obtain. Nature can be exceedingly harsh upon the cultivated

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plants which provide man's basic needs as well as upon those growing in the wild.

In the irrigated valleys of the West, salinity and varying soil moisture status are often prominent as environmental factors affecting crop development.

Elevated levels of soluble salts in soils adversely affect the growth of most plants (14). In many instances, one or more constituent ions in the salinity will have a specifically toxic effect on a given species. There is also evidence that salinity impairs crop response in direct relation to the increased level of osmotic pressure in the soil solution.

There is little quantitative data pertaining to the effect of soil salinity on the rate of leaf growth, -the rate of expansion of the photosynthetic surface. Yet, the extensive work of Watson (35) and others has shown that leaf growth is a primary determinant of crop yield.

Depletion of the soil moisture supply in the root zone down to the permanent wilting percentage has been frequently recorded as impairing crop growth (25). In many soils, there is a rather narrow range in moisture content between the 5-bar percentage and the 15-bar percentage (permanent wilting). This situation poses

difficulties in relating growth to soil moisture content at the higher levels of matric suction. Wadleigh and Gauch (33) showed that the rate of elongation per day of the main vein of cotton leaves, d_l/dt , approached zero as the matric suction in a Pachappa sandy loam approached its 15-bar percentage.

The study herein reported was undertaken to ascertain the interrelationship of varying osmotic pressure and varying matric suction upon the rate of expansion of the photosynthetic surface. An effort was also made to evaluate the effects of the ambient aerial environment upon the aforementioned relationship.

Castor beans were chosen as the experimental plant since rate of growth of the leaves is quite sensitive to environmental stresses. The species is relatively non-susceptible to plant pathogens and insect pests; and shows no specific toxic symptoms from NaCl added in moderately low levels to the soil substrate. Further, the leaves of this species will elongate 40 mm. a day under an amenable environment. This rapid rate of growth simplified collection of data on daily leaf elongation and the evaluation of said data.

Procedure

A two-ton batch of Pachappa sandy loam was taken from the surface ten inches of the field area

on the grounds of the U. S. Salinity Laboratory, Riverside, California. The soil was screened, thoroughly mixed, and spread out on the greenhouse floor to dry. When the soil had dried to a moisture content of 2.0 percent, 204.0 lb. lots were weighed out and added to 20-gallon oil drums. The drums were equipped with a one-inch opening on the side at the bottom. Before the soil was added, a large handful of pea gravel was placed in the center of the bottom of the drum. A piece of 1/4 inch Saran tubing connected from the center of the pile of gravel to the exterior through a rubber stopper in a hole in the side of the container at the base. This arrangement was made to facilitate subirrigation of the soil. The gravel, tubing and stopper were part of the tare weight of the drum.

Thus, each drum contained 200 pounds of soil at dry weight. Soil at this dryness packs readily, and the bulk density of the soil in the drums was 1.50-1.55.

On November 3, 1950, 20 grams of 16% superphosphate were mixed with the soil 4 inches below the surface in a 4 inch circle in the center. Ten grams of KNO_3 were placed in a ring at the outer edge of the soil surface. Four seeds of the Conner cultivar of castor beans were planted near the center. Each culture was then irrigated with 15 lbs. of Riverside tap water.

On November 27, a single seedling was selected in each drum for uniformity among all cultures and all other seedlings removed. The soil was then salinized by subirrigating with 24 pounds of water containing various levels of sodium chloride as shown in Table 1.

TABLE 1
LEVEL OF ADDED SALINITY IN SOIL

Added Salt as Percent of Soil	Na Cl added in Subirrigation gms.
0	0
0.025	43.5
0.05	87.0

On December 5, four tensiometers with mercury manometers were installed in each drum: one with the cup 3 inches deep; two with cups 10 inches deep on opposite sides of drum, and one with the cup 18 inches deep. The weight of the tensiometers were added to the tare weight of the drums.

On November 30, the first true leaves were becoming evident. Length of the main veins of true leaves were measured in millimeters every morning between 8 and 9 a.m.

Tensiometers were read each morning between 9 and 10 a.m.

The cultures were weighed each morning between 9 and 10 a.m. by use of an overhead torsion balance providing readings that were reproducible to 1/10 of

a pound. As the plants grew, the tare weight was adjusted in some degree to compensate for the increase in green weight of the plants

The "wet" cultures were irrigated whenever the weighing indicated that contained soil moisture had been reduced to 12 percent (24 pounds of water). Enough water was added in each soil moisture regime to restore soil moisture percentage to 18. Irrigation was alternated between surge and subsurface so that salt would not concentrate at top or bottom of container.

Periodically during the course of the study, soil samples were removed from the cultures by a modified soil tube taking a core 1cm. in diameter. Samples were taken by 5 cm. horizons; and they were used to determine soil moisture content as well as the salt content by means of electrical conductivity of the 1:1 extract (a filtered extract from a suspension involving equal weights of distilled water and dry soil).

Much helpful guidance for the quantitative analysis of the data for leaf growth was attained from Richards'(24) excellent discussion of this subject.

Growth may be characterized by a number of different functions, but much use is made of the logistic equation. The simple logistic is expressed

by the equation:

$$W = \frac{A}{1 + ae^{-bt}} \quad [1]$$

where,

- W = the growth characteristic being measured
- A = the asymptote, or accumulation of growth at cessation
- a = a constant
- e = base of the natural logarithms
- b = the rate constant
- and t = the units of time

This may be converted to

$$\ln\left(\frac{A-W}{W}\right) = \ln a - bt \quad [2]$$

Since this form is linear in its constants, $\ln a$ and b are easily derived. This equation characterizes a symmetrical logistic wherein the inflection point occurs at the time when 1/2 the growth has occurred and 1/2 the elapsed time for growth has occurred. Few growth phenomena take place so precisely. However, equations [1] and [2] have the advantage that the rate function, b , provides a comparative index of treatment effects on growth response.

It became clear after extensive exploration that accumulated elongation of the leaves had to be analyzed as non-symmetrical logistic curves if a reasonable fit were to be attained. This general formula used was:

$$L = \frac{S}{1 + e^{(a + bt + ct^2 + dt^3)}} \quad [3]$$

- Where L = daily length of the main rib of a given leaf in millimeters
 S = the asymptote of length for a given leaf
 e = base of natural logarithms
 a, b, c, d = derived constants
 t = time in days

$$\text{Hence, } \ln\left(\frac{S-L}{L}\right) = a + bt + ct^2 + dt^3 \quad [4]$$

Since equation [4] is linear in its coefficients, it made for simplicity in the derivation of the constants.

On differentiation, equation [3] becomes:

$$dL/dt = -\frac{L}{S} (S-L) (b + 2ct + 3dt^2) \quad [5]$$

Growth per day was the actual entity studied.

However, values for L derived by means of equation [3] may be designated L' and daily increments as $\Delta L'$. It was found that the locus for a curve expressing equation [5] was virtually identical for one showing the trend of $\Delta L' / \Delta t$. Thus the daily relationships between ΔL and $\Delta L'$ were used to evaluate the daily trend in environmental factors.

Solar radiation and water evaporation have their effects upon the surface area of the leaves. Therefore, it seemed preferable to transpose the linear measurements along the midrib to an areal index of the leaf surface.

At the time of harvest, the area of each leaf was measured by a photoelectric apparatus. That is, data were attained to enable a reasonable transposition of daily length measurements to daily values for area of each leaf. Total leaf area for each plant on each

day was attained from the summation of individual leaf area values.

Let A represent total leaf area on a plant on a given day, and S the asymptote for leaf area on the plant. Then

$$A = \frac{S}{1 + e^{-(a + bt + ct^2 + ct^3)}} \quad [6]$$

Also, ΔA will represent the daily increments in total foliar surface derived from length measurements, and $\Delta A'$ the increments calculated from equation [6]. On plotting the data, the locus of the curve for the $\Delta A'$ values did not provide a fully satisfactory fit for the actual trend of the ΔA values. Using Hoerl's (15) information, an equation for the observed trend in ΔA values with time was selected. Thus,

$$\Delta A = Kt^a e^{-(bt + ct^2 + dt^3)} \quad [7]$$

Where

ΔA = daily increment in total leaf area

K = constant

t = time in days

and a, b, c, d = constants

On conversion

$$\ln \Delta A = \ln K + a \ln t + bt + ct^2 + dt^3 \quad [8]$$

This equation is linear in its constants which are easily derived.

The values for ΔA attained by using the derived constants in equation [7] are designated as $\Delta A''$.

The quotient $\Delta A / \Delta A''$ provides an index of the growth potential for each day. If ΔA exceeds $\Delta A''$, growing conditions for the leaves were better on that day than would be indicated by equation [7]. The inverse situation also holds.

The values of $\Delta A / \Delta A''$ were evaluated as a function of daily indices for a number of environmental factors. Thus,

$$\Delta A / \Delta A'' = K \cdot L^a \cdot T^b \cdot H_x^c \cdot H_n^d \cdot P^e \cdot S^f \quad [9]$$

Where,

K = a constant

L = daily solar radiation in langley's divided by the mean daily solar radiation for the experimental period.

T = the maximum daily temperature in degrees centigrade prevailing for at least 2 hours divided by the mean of this values for the experiment.

Hx = the maximum daily relative humidity expressed in percent prevailing for at least 2 hours divided by the experimental mean for these values.

Hn = the minimum daily relative humidity expressed in percent prevailing for at least 2 hours divided by the appropriate mean.

P = the average osmotic pressure of the soil solution in atmospheres calculated for a given day in a given culture divided by the experimental mean of the daily values used for osmotic pressure.

S = the average matric suction of the soil water in bars calculated for a given day in a given culture divided by the experimental mean of the daily values used for matric suction.

a, b, c, d, e, f = constants.

Obviously, it was essential to divide the daily values for each environmental input by the respective means, so that the independent variables in equation [9] would be dimensionless. In other words, it would have been absurd to multiply langleys x bars. Furthermore, if a given environmental factor is arbitrarily held at the experimental mean, it becomes zero in equation [9] and is conveniently dropped from the relationship. In other words, the effect of varying osmotic pressure on $\Delta A / \Delta A$ may be studied while all other environmental inputs are held at their means.

Values for minimum daily temperature were not included in equation [9] since these values were essentially constant over the experimental period.

Fisher (8) pointed out in 1921 the importance of the "relative growth rate" in the quantitative analysis of plant growth. Thus,

$$Q = \frac{1}{A} \cdot dA/dt \quad [10]$$

where Q = relative growth rate (expressed in percent in this paper)

A = the leaf area attained on a given day

and dA/dt = the rate of increase in growth on that day

As indicated in the discussion of equation [5], the values for $\Delta A / \Delta t$ can be satisfactorily

substituted^{1/} for those of dA/dt in equation [10]
 One may immediately recognize that Q may be expressed in percent since it is the amount of growth taking place on a given day divided by the growth that had been attained by that day.

In analyzing the data by equation [10] , constants were first derived determining Q as a function of A on the "control" plants, i.e., those without salt stress or elevated matric suction. It was necessary to plot these data as a function of attained leaf area rather than time, because plants under some degree of stress may attain the same leaf area if allowed enough time; but the values for Q on plants under stress will be reduced on a given day. Thus, A , accumulated area, is used as a biological measure of time.

It was found that,

$$Q = K \left(\frac{1}{A} \right)^a e^{-bA^2} \quad [11]$$

excellently expresses the relationship. In this equation,

K = a constant

A = accumulated leaf area

^{1/} Discussion of equation [5] deals with the relation between dL/dt and $\Delta L' / \Delta t$. The same logic applies for the relation between dA/dt and $\Delta A/dt$.

e = base of natural logarithms

and a and b = constants

On deriving the constants for equation [11] on the control plants, these constants were locked into the equations used for quantitatively expressing the effects of other experimental treatments. That is, one would expect an environmental stress to displace the locus of a point from the curve found for the "control" plants.

Environmental effects were evaluated by the equation:

$$Q = K \left(\frac{1}{A} \right)^a e^{bA^2} \cdot L^f \cdot T^g \cdot H_x^h \cdot H_n^i \cdot P^j \cdot S^k \quad [12]$$

where,

L , T , H_x , H_n , P , and S are as specified under equation [9]; a and b are constants derived for control plants by equation [11], and f , g , h , i , j , k are constants relating to the aerial environment.

Use of equation [12] permits data from all treatments to be pooled, if it seemed advisable, for example, to attain a general measurement of the effect of osmotic pressure. Such pooling of the data would be unfeasible in equation [9], since, in that procedure, treatment means were adjusted to unity for each treatment.

There were indications in the data that successive leaves up the stem behave differently in environmental response. Thus the Q values for each successive pairs of leaves up the stem were evaluated by a relationship analagous to that of equation [12]. There were also indications that the leaves varied in their responses at different periods of foliar expansion. To study this possibility, the data for leaves at different positions on the plants were segregated into three growth periods: a, early expansion; b, grand period of growth; and c, maturation.

It is immediately obvious that a number of the environmental factors prevailing in this experiment affect plant growth through their effects on the water economy of the plants. Records were kept on the daily water loss from each culture. During the early days of the experimental period, much of the water loss would have been evaporation from the soil surface. After the plants had attained appreciable growth, transpiration would account for most of the water loss. Consequently, the first 18 days of water loss records were eliminated from the study of daily evaporation so as to exclude the records when soil evaporation was dominant.

Daily evapotranspiration was evaluated by the equation:

$$E = K \cdot L^a \cdot T^b \cdot H_x^c \cdot H_m^d \cdot P^e \cdot S^f \cdot A^g \quad [13]$$

Where

E = daily water loss for a given culture
divided by the experimental mean for
daily evaporational losses

A = total leaf area per plant in cm^2 at time t ,
divided by the mean value M_A , for all leaf
area measurements

All other factors are as explained under equation [9].

In equation [13],

$$E = E_o / M_E \quad [14]$$

and,

$$A = A_o / M_A \quad [15]$$

where,

E_o = water loss in gms. per culture per day

M_E = mean of E_o values

A_o = leaf surface in cm^2 on a given plant
on a given day.

M_A = mean of A_o values

Hence, if environmental inputs are stipulated to be
at their mean values, then equation [13] becomes

$$E_o / M_E = K \left(\frac{A_o}{M_A} \right)^g \quad [16]$$

Differentiating,

$$dE_o / dA_o = M_E \cdot K \cdot \left(\frac{1}{M_A} \right)^g \cdot g A_o^{g-1} \quad [17]$$

Equation [17] permits the derivation of the
rate of water loss per unit leaf area for varying
foliar surface at stipulated levels of environmental
input. Analogous equations were derived for each
environmental factor at a given level of foliar surface.

BASIC DATA

Light

Climatological data of the U. S. Weather Bureau show that solar radiation (direct and diffuse) at Riverside, California, averaged 235.3 langley's per day during December 1950 and January 1951. A minimum value of 62 and a maximum of 353 were recorded during this period. The trend is shown in Figure 1.

Obviously, the experiment was carried out during a period of relatively low solar radiation. This situation was premeditated. As the data will show, if a comparable experiment were carried out at a time of relatively high solar radiation at Riverside, then the soil containers would have to be 4 to 5 times as large as the 20-gallon oil drums that were used. This would be essential to attain meaningful soil moisture data under the higher rate of evaporation under high solar radiation.

A recording pyrliometer was maintained in the greenhouse during the experimental period. The records attained are far more detailed than can be effectively used in the mathematical analyses herein reported. These records did show that solar radiation inside the greenhouse was only 75-80 percent of that outside. This point is essential to keep in mind on interpreting the data: records for outside solar radiation were not converted by use of the aforementioned factor to greenhouse conditions. However, there was no dearth of

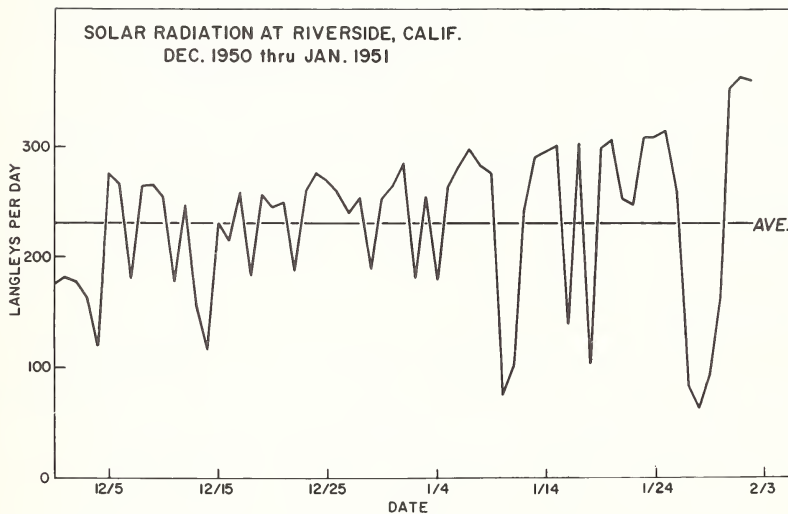


Figure 1

Daily solar radiation at Riverside, California,
during December 1950 and January 1951

advective energy impinging upon the experimental plants within the greenhouse. This house had a large expanse of dry cement floor, forced air circulation, and few other plants than those in this experiment. On many days, the evaporating power of the air in the greenhouse undoubtedly exceeded that potentially available from solar radiation outdoors. Halstead and Covey (12) showed that under field conditions actual evaporation can exceed that possible from net radiation by a considerable amount. This is the "Oasis" effect.

Temperature

A hygrothermograph was maintained in the greenhouse near the experimental plants and appropriately protected from direct solar radiation. From the thermographs, the maximum temperature that prevailed for two hours each day as well as the minimum temperature for an analogous period was determined. As shown in Figure 2, these specified values for maximum temperature varied from 20° C to 39° C with a mean of 28.0° C. The minimum temperature values ranged from 13° C to 19° C with an average of 17.6° C. There was some malfunctioning of the air-conditioning equipment during a few nights in early December 1950 so that minimum values for night temperature dropped as low as 13° C; but for most of the duration of the experiment, minimum values for

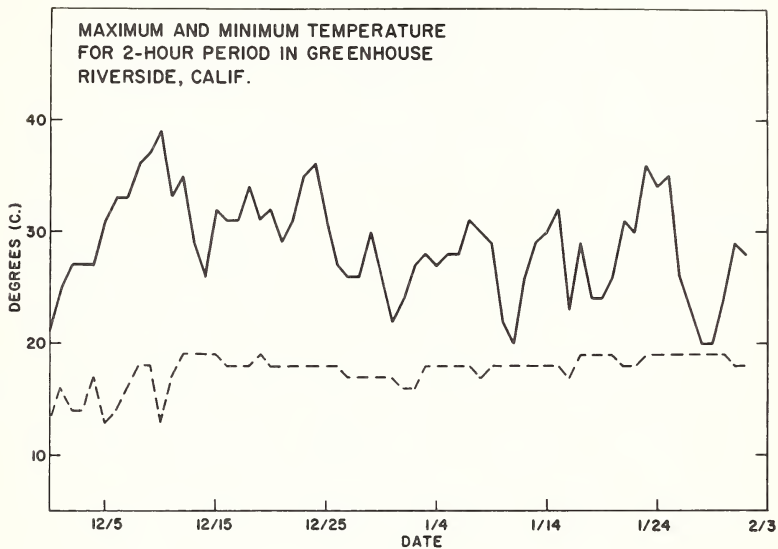


Figure 2

Maximum and minimum daily temperature
during the experimental period

night temperature were rather constant at 18° C. Accordingly, this environmental input was not included as a variable in the multiple regression equations that were derived for quantitative evaluation of the impact of the aerial environment upon observed experimental responses.

Humidity

Figure 3 shows the values for maximum relative humidity that were attained over a 2-hour period for each night during the course of the experiment; as well as the values for minimum relative humidity attained for a 2-hour duration for each day. Maximum humidity readings varied from 29 to 100 percent with an average of 54.8 percent. Minimum relative humidity values ranged from 15 to 64 percent with an average of 33.0 percent.

Intercorrelation Between Attributes of the Aerial Environment

Obviously, levels of daily solar radiation would be a main determinant of the daily levels of temperature and humidity. This was shown by the following correlation coefficients:

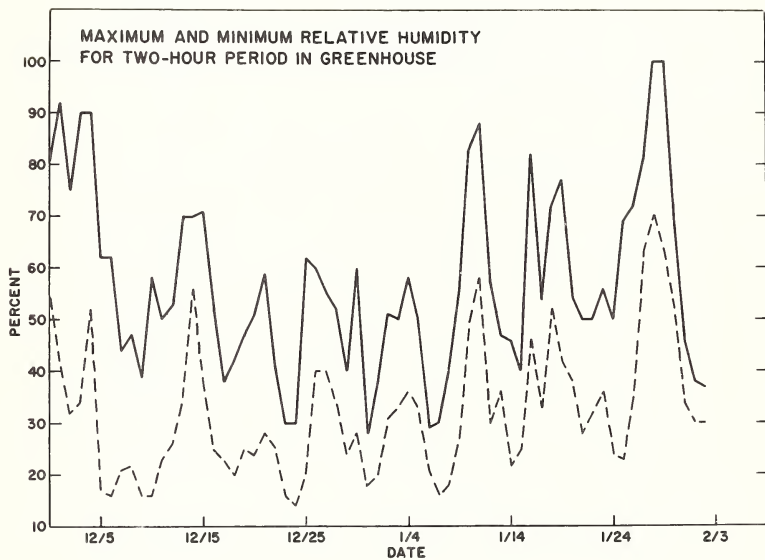


Figure 3

Maximum and minimum relative humidity
during the experimental period

TABLE 2
INTERCORRELATION AMONG INDEPENDENT VARIABLES

Correlated variables	r	r ²
		Percent of total variance accounted for
Light X Max Temperature	0.678**	46.0
Light X Average Relative Humidity	-0.671**	45.0
Max. Temp. X Average Relative Humidity	-0.627**	39.3

** = Significant at the 0.01 probability level

These statistics show that solar radiation was the main determinant of the variance in the values for both temperature and humidity; and that variance in the readings for light and temperature accounted for most of the variance in the values for relative humidity. Hence, one could expect that relative humidity would have little impact as an independent variable in a multiple regression equation evaluating aerial environment upon experimental response.

Matric Suction of the Soil

Figure 4 shows the relationship between the average of the tensiometer readings and the percent of moisture in the soil as determined by daily weighings in the "No salt-dry" cultures. This curve follows

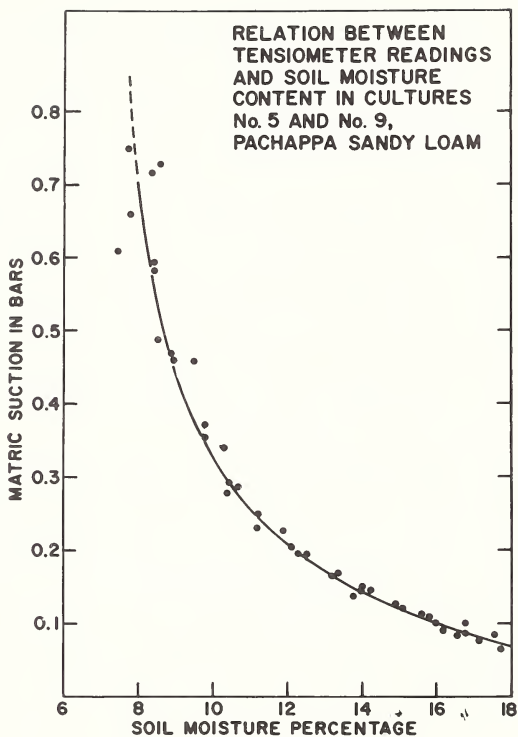


Figure 4

Observed relation between soil moisture percentage
and average tensiometer reading in the
"no salt - dry" cultures

very closely the trend for the values attained in this sample of soil by evaluation with a pressure-plate apparatus. The moisture characteristic curve relating matric suction to soil moisture percentage from the 15 bar percentage down to low levels of matric suction is shown in Figure 5. The day to day values for matric suction were taken from the average of the tensiometer readings at values of 0.7 bars or less. At higher values of matric suction, the curve in Figure 5 was used. Moisture content of the soil determined by weighing was transposed to the comparable value for matric suction using this curve.

The value for the 15-bar percentage was checked by growing 3 castor bean plants in a 20 gallon drum filled with the soil used in the experiment. When the plants attained a height of about 30 inches, they were allowed to deplete the soil moisture to the stage wherein the plants were permanently wilted. At that stage, weighing of the drum of soil revealed that it contained 5.55 percent soil moisture. This is an unusually close check of the 15-bar percentage.

Figures 6, 7, 8 show the observed values for matric suction in a representative culture from each of the 6 treatments. During the latter part of the experimental period, the soil moisture tension on the "no salt - wet" culture reached higher values than intended. Transpiration from the large plants would

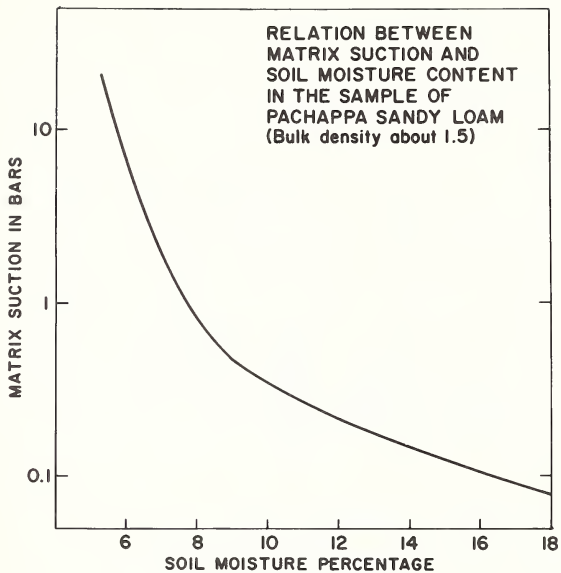


Figure 5

Relation between soil moisture percentage and matric suction in sample of Pachappa sandy loam

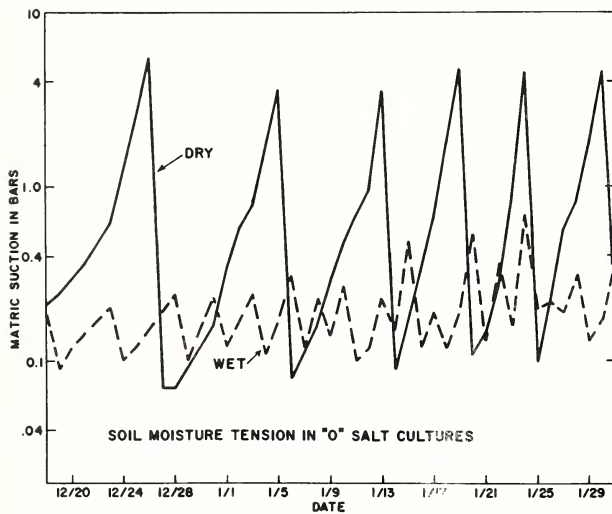


Figure 6

Daily readings of matric suction in the "no salt" cultures

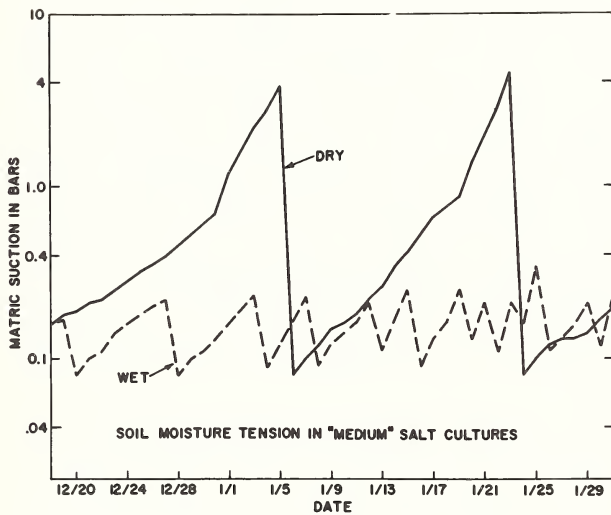


Figure 7

Daily readings of matric suction
in the "medium salt" cultures

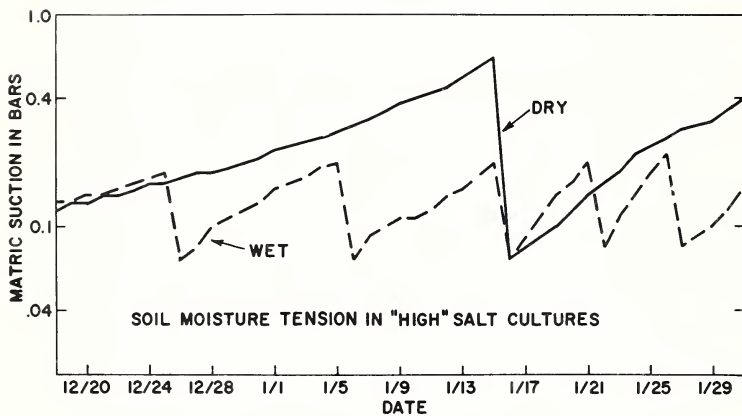


Figure 8
Daily readings of matric suction
in the "high salt" cultures

remove 3.5 - 4.5 liters of water from the 90.7 kilogram (200 pound) mass of soil in one day's time. Thus, water depletion exceeded the target level (0.25 bars of matric suction) on several occasions. Figure 6 also shows that the matric suction in the "no salt - dry" cultures did not attain as high a level prior to irrigation as had been planned (10-12 bars). During the course of the experiment, it was decided to accept a lower value for terminal matric suction in the "dry" cultures rather than permit the plants to even show signs of incipient wilting. No experimental plant ever wilted during the course of this study.

Values for matric suction in the "med. salt - wet" cultures were largely within the target range. In the "med. salt - dry" cultures, matric suction did not attain as high a value as desired prior to irrigation. These cultures were irrigated only twice during the experimental period; that is, a modest level of salinity was associated with a reduced rate of water depletion from the soil by the plants.

The "high salt" cultures (Figure 8) were well within the target range in the "wet" series; but did not attain near as high a value for matric suction in the "dry" series as would have been preferred. Growth of the plants stopped prior to the one irrigation that was provided.

At the lower values of soil moisture percentage, appreciable change in the calculated value for matric suction could take place over a 24 hour period (9 o'clock one morning until 9 o'clock the next). The question arose as to what value for matric suction should be taken for a 24 hour period to relate to growth or evaporation during that period. Many observations on tensiometers reveal that over a 24 hour period they reach a maximum reading late in the afternoon with an appreciable lowering of the tension over night so that the morning reading is appreciably less than the one occurring the previous afternoon. Thus, the morning reading was taken as a fairly good average of the range in matric suction values that occurred during the previous 24 hours.

Salinity Of The Soil

The selection of a single value that characterizes the salinity of the soil in the root zone of a plant during the course of a given day is not a simple matter (31, 32). Salt moves in a soil as its vehicle water, moves. Plant roots preferentially remove water from zones of lower salt content (5, 19, 34). In a soil, this action of the roots in preferentially absorbing water with the higher level of free energy tends to incur an equalization of the free energy of the soil water over the root zone (34).

Table 3 provides information on the salinity of the soil in cultures varying as to level of added NaCl. The $EC_{1:1}$ ^{1/} for the "no salt" cultures arose from added plant nutrients and small amounts of solubles present in the original batch of soil. The last column on the right gives values for salt content of cultures used in the multiple regression analyses. On a 1:1 basis, 90.7 kilograms of dry soil would be mixed with 90.7 liters of water. Thus, the figures in the right hand column were attained by multiplying respective values in the preceding column by 90.7 and rounding off, since the calculation involves some inherent errors. These figures were used to calculate the prevailing osmotic pressure in the solution of each culture at varying soil moisture contents.

Figure 9 shows the concentration of NaCl in the salinized cultures at various soil moisture percentages; and Figure 10 the calculated (17) osmotic pressure due to added NaCl. As indicated in the discussion of Table 3, total osmotic pressure of the soil solution must include the effect of added plant nutrients. Thus Figures 11 and 12 show the daily trend of calculated osmotic pressures in a representative culture

^{1/} Electrical conductivity of an extract of a 1 to 1 suspension of soil and water.

TABLE 3
SALINITY OF SOIL CULTURES

Salinity levels	NaCl added per culture	NaCl added per culture	Range in values for EC 1:1	Range in values for conc. of 1:1 extracts	Aver. value for conc. of 1:1 extracts	Salt per culture used in Math. analyses
	gms.	Mille-equivalents	Micromhos/cm.	M.E./liter	M.E./liter	M.E./culture
"0"	0	0	230-370	2.3-3.7	2.9	260
"med"	43.5	744	690-1600	6.9-15.2	10.9	1000
"high"	87.0	1488	1050-2900	10.5-29.0	18.6	1700

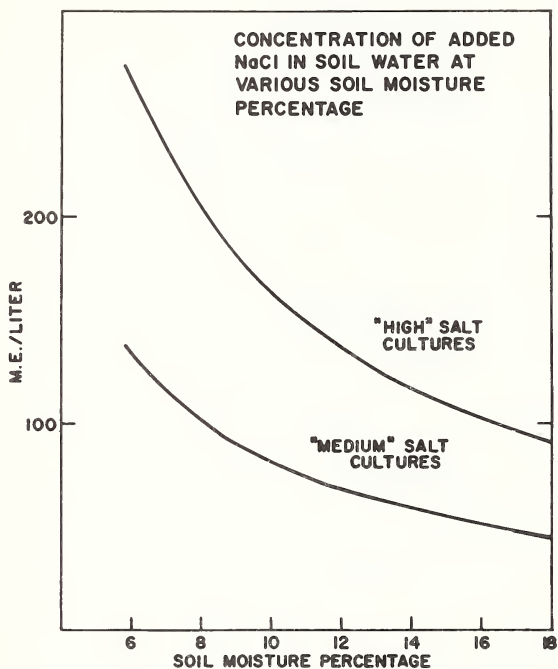


Figure 9

Concentration of added NaCl in soil water as a function of soil moisture percentage

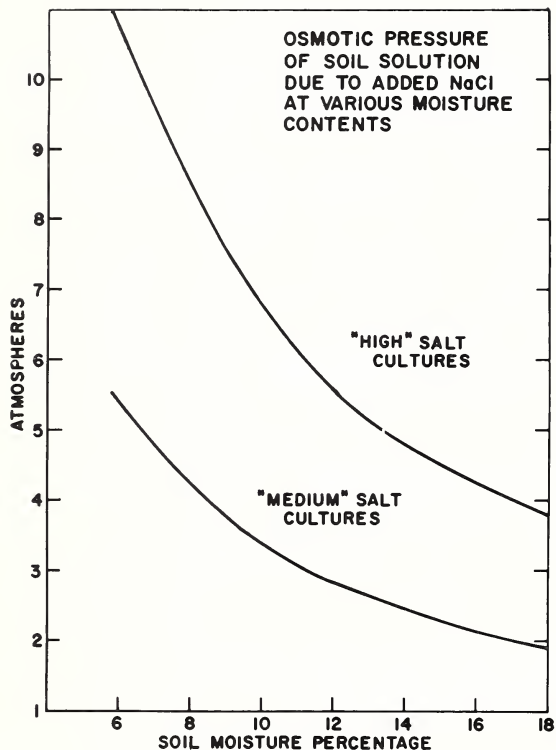


Figure 10

Average osmotic pressure of soil solution due to added NaCl as a function of soil moisture percentage

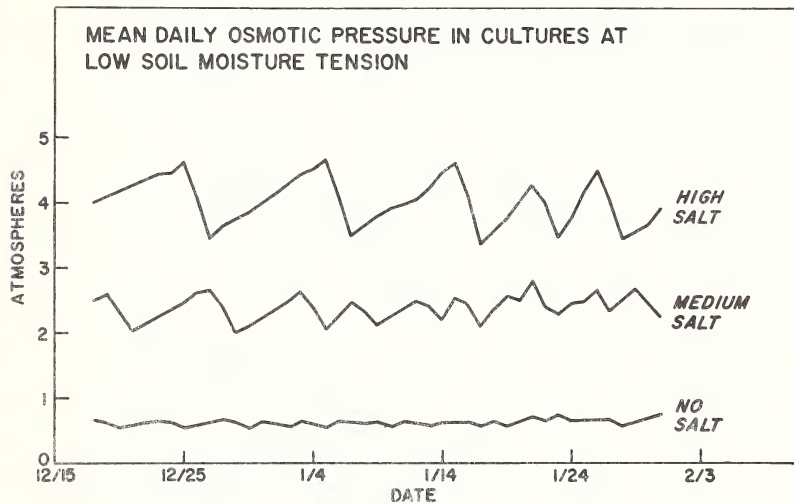


Figure 11

Daily mean value for osmotic pressure of the
soil solution in the "wet" cultures

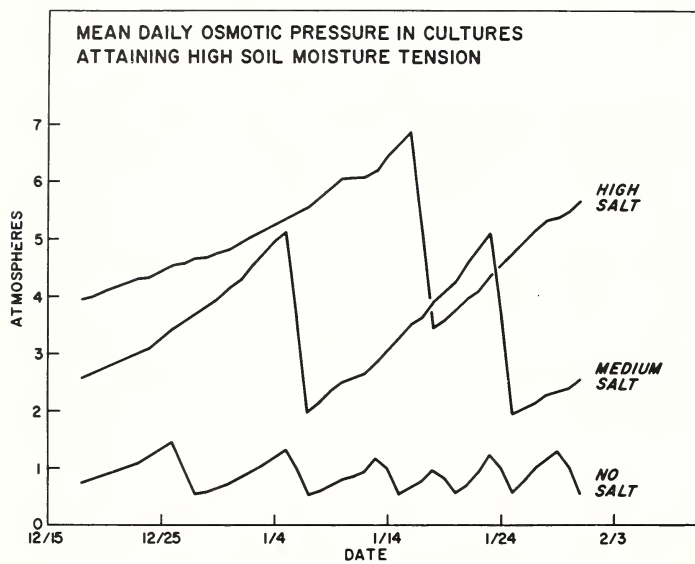


Figure 12

Daily mean value for osmotic pressure of the
soil solution in the "dry" cultures

from each of the six treatments. One could anticipate that variability in osmotic pressure in the "no salt-wet" cultures would not be a factor in plant performance, but could be a significant determinant in some of the other treatments.

Total Soil Moisture Stress

A fellow scientist at the Salinity Laboratory, R. G. Campbell, removed soil samples from a few of the cultures on days when the prescribed maximum in soil moisture stress was supposedly attained. Decrease in free energy of the soil water was determined by a freezing-point-depression procedure developed by Richards and Campbell (26). Representative data are presented in Table 4. The main variability in the values presented for each culture was incurred by whether the sample was removed from the north or the south side of the drum. For a given side of the drum, total soil moisture stress was remarkably uniform down through the horizons.

It is most significant that the average values for total soil moisture stress determined by freezing point depression were about 2 atmospheres higher than those calculated by adding the matric suction in bars to the osmotic pressure values calculated from salt concentration in the soil water. In evaluating the

TABLE 4
TOTAL SOIL MOISTURE STRESS IN SOIL SAMPLES
Culture No.

Soil Horizon	7 - (high salt-wet) Sampled on 1/8		2 - (high salt-dry) Sampled on 1/16		11 - (medium salt-wet) Sampled on 1/16	
	South side	North side	South side	North side	South side	North side
0-2"	atmos.	atmos.	atmos.	atmos.	atmos.	atmos.
	7.61	4.84	16.1	15.3	4.04	4.58
2-4"	8.05	4.60	10.1	12.4	5.40	4.56
4-6"	8.89	4.70	9.25	10.6	6.05	4.56
6-8"	9.39	5.96	9.64	8.95	6.54	4.40
8-10"	9.59	5.14	10.2	8.53	6.50	4.75
10-12"	9.05	4.65	9.55	8.60	6.10	4.35
Ave.	6.87		9.5 (top horizon excepted)		5.15	
Value for Osmotic pressure on day specified	4.56		6.87		3.16	
Value for matrix suction on day specified	.19		.63		.26	
Calculated Total soil Moisture Stress	4.75		7.50		3.42	

data for plant response, no attempt was made to relate the values from the studies on freezing point depression. No explanation for this discrepancy is offered.

Water Content of Soil

Precision for the calculated values for osmotic pressure of the soil solution was much dependent on the precision of the weighing procedure for determining total water content of a given soil culture. Table 5 provides a sample of the data comparing soil moisture percentage determined by weighing the drums with that determined by soil sampling. There was usually recorded considerable range in the soil moisture percentage in the soil mass at a given time of sampling, especially in the salinized cultures. Salt pockets are associated with higher levels of soil moisture (34) due to differential rate of water extraction by the roots.

Adjusting Tare Weights

The tare weight of each culture was adjusted upward during the course of the experiment on an arbitrary basis in order to allow for the increase in weight of the plant. If this had not been done, the close agreement between systems of determining soil moisture percentage would not have prevailed.

TABLE 5
SOIL MOISTURE PERCENTAGE IN CULTURE NO. 11

Date of Determination	By Weighing	Average of 8 small soil samples per culture	Range for samples	
	Percent	Percent	Percent	
1/ 5/51	12.85	13.1	11.9	- 15.2
1/ 9/51	12.10	12.2	9.95	- 14.40
1/13/51	13.10	12.9	10.8	- 15.1
1/23/51	11.05	11.3	7.8	- 13.8
1/27/51	11.60	11.5	7.2	- 14.2

The increase in tare allowed for plant growth is shown in Table 6, along with the actual green weights of the plants at the time of harvest. Increases in tare weight were usually 0.1 to 0.3 lbs. at each time of irrigation during the course of the study. For example, tare weight of the "no salt-wet" cultures was increased 0.2 lbs. at time of each irrigation. The adjustments in tare due to plant growth was a good approximation in most of the treatments except those for "no salt-dry". The investigator was capable of making some poor guesses.

Green Weight of Plants at Harvest

The summation of the daily increment growth is well indicated by the total weight of plant tops at harvest. Table 7 provides growth data for the respective plants at termination of the experiment on Feb. 1, 1951. The two plants in each treatment were satisfactorily similar in total growth response and treatments had major effects on growth. Leaf blades made up a remarkably constant percentage of the total green weight of the tops. In other words, foliar surface in relation to total mass of tops was not a significant variant in experiment. There was an apparent tendency for the dry matter percentage of leaves to increase with increasing soil moisture

TABLE 6

GREEN WEIGHTS OF EXPERIMENTAL PLANTS AT HARVEST AND
ADJUSTMENTS IN TARE WEIGHTS OF CULTURE DUE TO PLANT GROWTH

Treatment	Culture No.	Green wt. of tops	Allowance for roots (15%)	Total green weight	Total increase in tare weight
		gms.	gms.	gms.	lbs.
"No salt - wet"	6	1425	214	1639	1632
	12	1358	204	1562	1632
"No salt - dry"	5	1075	161	1236	835
	9	1042	156	1198	697
"Med. salt - wet"	3	861	129	990	907
	11	985	148	1133	998
"Med. salt - dry"	1	342	51	393	227
	10	446	67	513	317
"high salt - wet"	4	330	50	380	363
	7	454	68	522	500
"high salt - dry"	2	144	22	166	91
	8	123	19	142	91

TABLE 7

GROWTH DATA FROM PLANTS
AT TERMINATION OF THE EXPERIMENT

Treatment	Cul- ture No.	Green weight stem gms.	Green weight of petiols gms.	Green weight of leaves gms.	Green weight of residue gms.	Dry wt. of leaves gms.	Dry wt. of leaves percent	Green wt. of plant tops gms.	Leaves as percent of total green wt.
"No salt - wet"	6	536.0	376.8	496.7	15.2	89.9	18.1	1425	34.9
	12	490.0	366.3	468.0	33.2	87.1	18.6	1358	34.5
"No salt - dry"	5	392.0	289.9	381.1	11.8	73.6	19.3	1075	35.5
	9	377.0	277.7	369.6	17.9	71.7	19.4	1042	35.5
"Med. salt - wet"	3	329.0	199.2	324.0	8.4	65.4	20.2	861	37.6
	11	380.0	267.1	326.6	11.4	67.9	20.8	985	33.2
"Med. salt - dry"	1	132.0	83.6	123.6	3.2	23.7	19.2	342	36.1
	10	179.0	120.1	145.1	1.9	28.7	19.8	446	32.5
"High salt - wet"	4	141.0	70.5	112.0	6.1	22.5	20.1	330	34.0
	7	181.0	112.8	156.7	3.5	33.5	21.4	454	34.5
"High salt - dry"	2	62.0	31.9	49.3	1.0	10.2	20.7	144	34.2
	8	46.0	28.4	45.7	3.2	10.8	23.7	123	37.1

stress, particularly in relation to increased salinity. However, analysis revealed that none of the treatment effects on percentage dry matter were statistically significant. Mean standard deviation of treatment effects was 1.08.

As shown in Table 8, there were very real differences in accumulated green weight of tops between all treatment inputs with no valid evidence of an interactive relation between soil moisture regimes and salinity levels. That there were such major differences in the values for accumulated growth, provides much greater validity for analysis of the day to day increments in growth.

Leaf Elongation

Over 3500 measurements of leaf length were made during the course of the study, and it is not feasible to present all these data. Figure 13 shows the data for elongation for a few of the leaves on control culture No. 6. The loci of the respective curves was determined by use of equation [3]. The fit was very good. As shown in Figure 14, the maximum length of the leaves increased remarkably up the stem with the maximum length being observed for the eighth leaf on the control cultures.

TABLE 8

SIGNIFICANCE OF TREATMENT MEANS FOR TOTAL
GREEN WEIGHT VALUES FOR TOPS OF PLANTS

Treat- ment	"0" salt	"Med." salt	"High" salt	Pooled effect of salinity
	gms.	gms.	gms.	gms.
"wet"	1392	923	392	902
"dry"	1059	394	134	529
Average of "wet" and "dry"	1225	659	263	

Mean Standard Deviation = 69.0

<u>Treatment Comparisons</u>	<u>Variance Ratio*</u>
Soil moisture levels	87.9
Salt levels	196.6
Soil moisture x Salt	4.1

*Variance ratios for the 0.05 and 0.01 levels of
probability are 6.61 and 16.26 respectively.

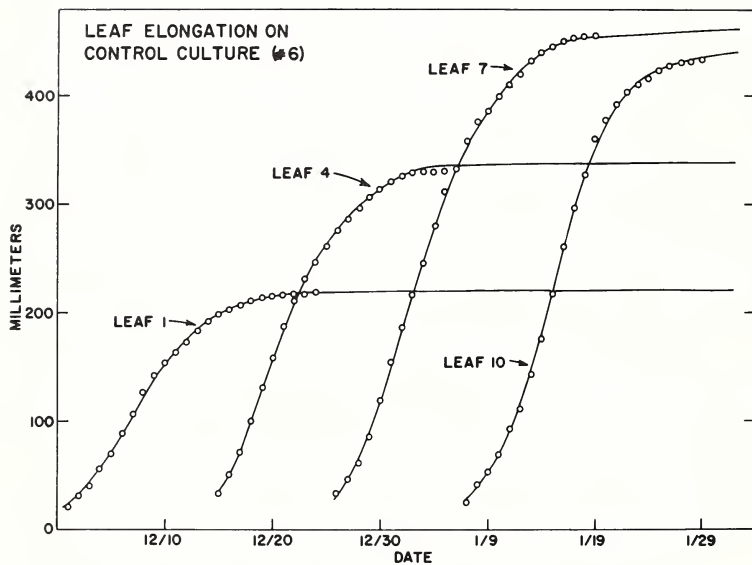


Figure 13

Daily growth of selected leaves of plant #6
on the "no salt - wet" treatment

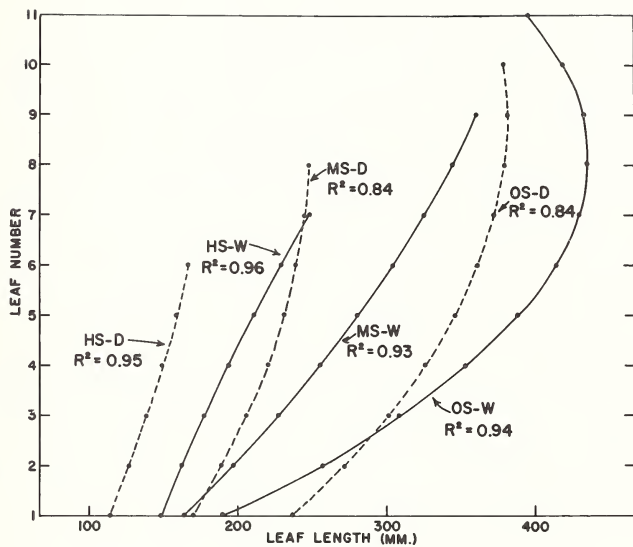


Figure 14

Derived values for ultimate growth of leaves
on the various treatments

The curves in Figure 14 were fitted by 2nd degree parabolic equations to the maximum lengths of leaves for each culture. The values for R^2 ^{2/} show that a very good fit was attained for each treatment. For example, 94 percent of the variance in maximum leaf lengths for the control plants was accounted for by using the parabolic equation reflected by the curve labelled "OS-W". Table 9 presents the constants for the equations for the six treatments. The matrix in Figure 14 may be readily expressed by a mathematical model involving leaf position (N), salinity (S), and soil moisture regime (T). Arbitrary values were given to the S and T levels prevailing. The empirical equations predicting each constant in the relationship expressing maximum length of leaf ($L_M = a + bN + cN^2$) are given at the bottom of Table 9. The precision of prediction shows that the relationships were not occurring at random.

The foregoing information is not of major physiological significance. However, one can assume that the locus of the curve for the control

^{2/} As defined by Ezekiel and Fox (7), R^2 , the index of determination, indicates the proportion of variance in the dependent variable that is accounted for by concomitant variance in the independent variables.

TABLE 9

CONSTANTS FOR EQUATIONS
SHOWING RELATION OF MAXIMUM LEAF LENGTHS (L_M)
TO TREATMENTS AND POSITION ON STEM (N)

$$L_M = a + bN + cN^2$$

Treatment	a	b	c	Values for	
				Moisture tension T	Salinity level S
No salt - wet	116.0	78.69	-4.847	0	0
Med. salt - wet	129.4	35.87	-1.137	0	1
High salt - wet	132.1	14.46	+ .280	0	2
High salt - dry	198.5	40.96	-2.303	1	0
Med. salt - dry	147.1	23.99	-1.437	1	1
High salt - dry	100.2	14.42	-.580	1	2
a = 118 + 80T + 8S - 57 ST				$R^2 = 99.4$	
b = 75 - 36T - 32S + 19ST				$R^2 = 96.9$	
c = -4.50 + 2.20T + 2.55S - 1.69ST				$R^2 = 94.0$	

plants (OS-W) was largely determined by the genetic potentialities of the species growing in a relatively amenable environment. Displacement of the other curves in Figure 14 from the locus of that of the "control", could almost be fully accounted for by linear responses to salinity and soil moisture regime (equations at bottom of Table 9). This point is important in that it again emphasizes that the imposed treatments were highly effective and relatively consistent in modifying growth response.

Figure 15 compares the elongation of the 5th and 8th leaves in the "wet" treatment vs. the "dry" treatments in the absence of added salinization. Leaves on culture #5 would nearly stop growing when the matric suction reached about 5 bars. They would make rapid growth upon irrigation, but the maximum elongation was always less when elevated soil moisture tension was imposed. This point is also shown in Figure 14. It should be noted in this latter Figure that in the curve "OS-D", the first two leaves reached maximum length before an appreciable level of matric suction developed in the soil.

The effect of increasing salinization in the "wet" cultures on elongation of the seventh leaf

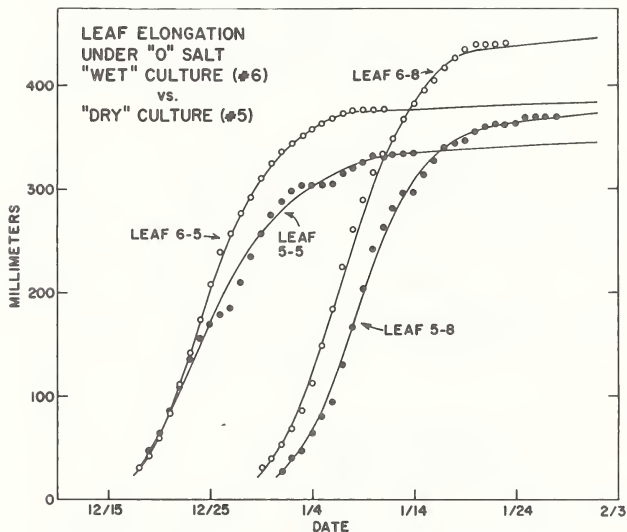


Figure 15

Daily growth of selected leaves from plants on the "no salt - dry" treatment as compared to those on the "no salt - wet" conditions

is shown in Figure 16. Increased salinity was associated with a significant delay in the appearance of the seventh leaf, marked reduction in rate of growth, and a decreased maximum for leaf length. Similar effects were found for salinity levels within the "dry" cultures as shown in Figure 17, but growth was even further depressed at a given salt level.

Transposition of leaf data to surface area

It was deemed preferable to relate environmental stresses to areal surface of the leaf, rather than to the length measurements that were made. Light absorption and evaporation are both directly related to surface area.

At the termination of the experiment on February 1, 1951, the area of each leaf on each plant was measured by a photo-electric planimeter. Many of the castor bean leaves were as broad, or broader, than they were long. The surface area approached a circle. Accordingly, leaf area (A) in cm.^2 was calculated from leaf length (L) in mms. by the following equation:

$$A = \left(\frac{L/10}{2} \right)^2 \times 3 \quad [18]$$

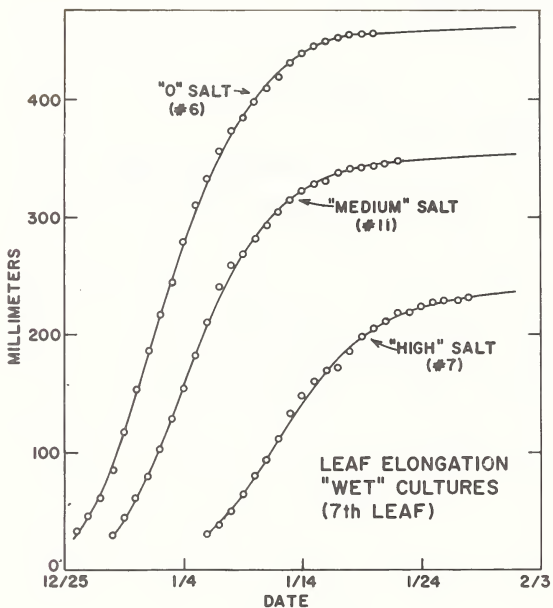


Figure 16

Daily growth of the 7th leaves from the
"wet" cultures at three salt levels

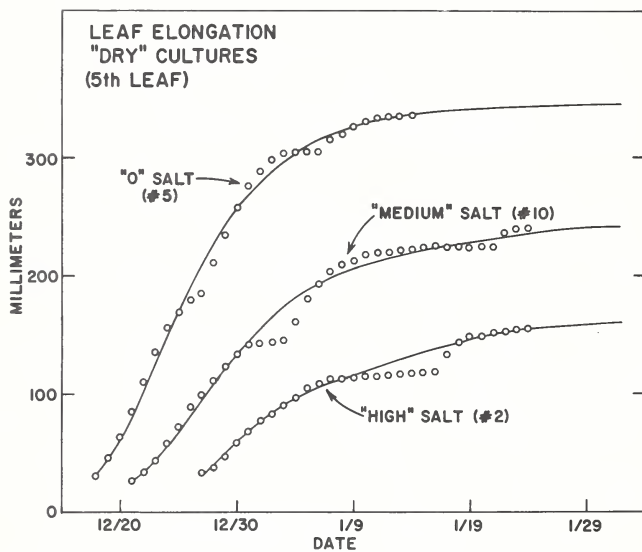


Figure 17

Daily growth of the 5th leaves from the
"dry" cultures at three salt levels

That is, the square of $1/2$ the length in cms. was multiplied by 3 rather than 3.1416. High precision was not justified and the area of most leaves appeared to be slightly less than that of a true circle. Figure 18 shows a fairly close relationship between the calculated and measured values.

Equation [18] was used to convert each record of leaf length in mms. to leaf area in cm.^2 . Since a number of quantitative studies were made that involved the total calculated leaf area on each plant, it is of interest to note that Table 10 reveals a very close relationship between total leaf area measured at terminus of the experiment and total leaf area calculated. The photoelectric device used for measuring area did not have the ultimate in precision.

Daily Water Loss From Cultures

Figures 19 and 20 show the high degree of variability in water loss per day over the experimental period with a general increase in rate of evaporation as the plants grew larger. The daily weighing procedure revealed water losses as low as 40 grams per day and exceeding 5 kilograms per day. The range of values is shown in Table 11.

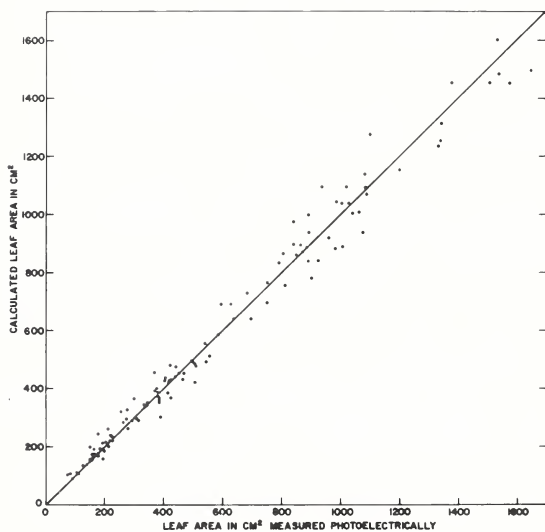


Figure 18

Relation between values for total areas of leaves derived photoelectrically as compared with the calculated values

TABLE 10
CALCULATED VERSUS MEASURED LEAF AREA

Treatment	Plant No.	Total leaf area measured cms ²	Ratio <u>meas.</u> <u>calc.</u>	Total leaf area calculated cms ²
No salt - wet	6	12612	.975	12941
	12	11885	.996	11936
Med. salt - wet	3	6431	1.047	6141
	11	6601	1.041	6340
High salt - wet	4	3375	.982	3436
	7	3760	1.071	3512
No salt - dry	5	8019	.951	8435
	9	7546	.995	7577
Med. salt - dry	1	2945	1.009	2920
	10	3407	1.033	3297
High salt - dry	2	1415	1.004	1410
	8	1297	.954	1360

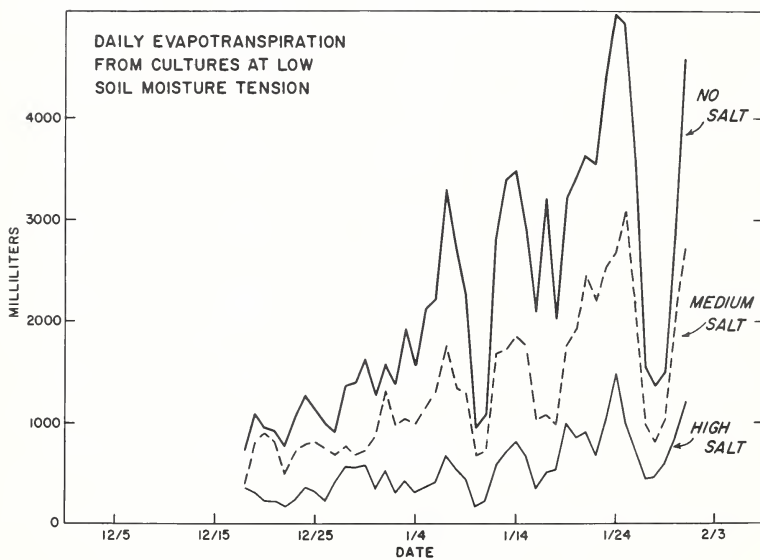


Figure 19

Daily evapotranspiration from cultures maintained
at low soil moisture tension

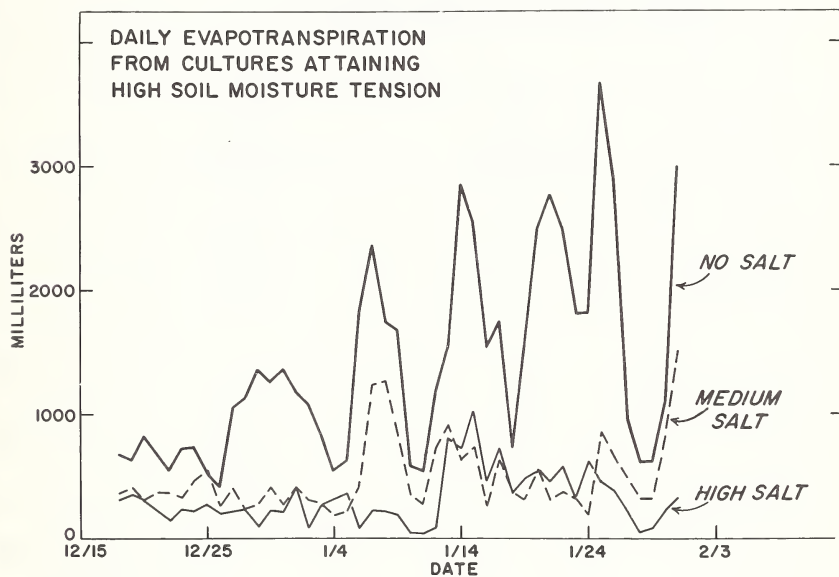


Figure 20

Daily evapotranspiration from cultures permitted to attain high soil moisture tension

TABLE 11
RANGE IN VALUES FOR DAILY WATER LOSS
FROM THE VARIOUS TREATMENTS

Treatment	Low value	High value
	gms/day	gms/day
No salt - wet	720	5080
Med. salt - wet	350	3360
High salt - wet	180	1770
No salt - dry	220	3670
Med. salt - dry	180	1860
High salt - dry	40	1040

ANALYTICAL FINDINGS

Evapotranspiration

As aptly emphasized by Kramer (16), Gardner (10), Slatyer (28), and others, environmental factors affecting water supply to and depletion from the plant have their effect on growth through their intermediary effect upon the physical status of water within the plant. It is appropriate, therefore, to first consider the findings with respect to water loss by soil evaporation and transpiration from the variously treated cultures.

It is important to keep in mind the excellent diagram presented by Philip (22). The diffusion pressure deficit (DPD) in the soil water may vary from essentially 0 to values up to and even exceeding 25 atmospheres. Root cells may make some adjustment to increasing DPD in the soil by an increase in DPD of the absorbing tissues (6). The ambient atmosphere around a leaf may vary in DPD from 0 to over 1200 atmospheres. The desiccating power of the air may permeate into the exterior of the spongy parenchyma cells within the leaf. Thus, a plant growing in a dry soil on a hot, dry day may be subjected to terrific stresses that impose internal water deficits which in turn affect cellular multiplication and expansion.

The available data were analyzed by a computer programmed to provide the constants of equation [13]. The experimental means used in normalizing the data for this equation are given in Table 12. In actual computation, equation [13] was converted to the logarithmic form so that the exponents became regression coefficients in an equation linear in its constants. That is, equation [13] becomes,

$$\ln E = \ln K + a \ln L + b \ln T + c \ln H_m + d \ln H_x + e \ln P + f \ln S + g \ln A. [19]$$

Some of the findings with respect to evapotranspiration are presented in charts as the linear regressions derived from equation [19] since this was the basis on which the computations were made. Conversion of the results to the anti-logarithmic form of equation [13] provided curves that may as much reflect the mathematical manipulation as the physiological response of the plants.

Table 13 represents statistics for the data attained from equation [19] within each of the six treatments.

There was a remarkable degree of uniformity in the regression coefficients associated with leaf area among the 6 treatments (range = 0.447 to 0.695). This is illustrated by the regression lines in Figures 21 and 22. The standard errors associated with the regression coefficients for leaf area (Table 13) tended to be smaller than those for other independent variables. This

Table 12

Factor means used for normalizing the observations
for use in equation [19]

Factor	Mean value
Water loss per day	1056 gms
Total leaf area per plant per day	3233 cm. ²
Solar radiation per day	235.3 langleys
Maximum temperature	28.02 °C.
Mean daily osmotic pressure	2.709 atmos.
Mean daily matric suction	0.4685 bars.

Table 13
Evaporation Coefficients

Treat- ment	Coef.	"Independent" factors							ln K	R ² %
		Light	Temp.	H min	H max	O.P.	M.S.	Leaf area		
OS-W	Regress. ^{1/}	.478	.850	-.00015	-.00017	-.181	.034	.672		
	S. E.	.058	.161	.093	.089	.309	.049	.026	-.1006	93.5
	F	66.9**	27.9**	.03	.04	.34	.48	658.6**		
MS-W	Regress.	.517	.834	-.00021	-.0011	-.597	-.021	.641		
	S. E.	.085	.226	.077	.128	.340	.077	.035	-.2686	86.9
	F	38.9**	13.6**	.08	.75	3.08	.08	327.5**		
HS-W	Regress.	.466	.870	-.00055	-.00026	-2.66	.398	.505		
	S. E.	.113	.303	.173	.169	.611	.179	.050	1.3117	76.4
	F	17.1**	8.22**	.10	.02	19.0**	4.96*	100.6**		
OS-D	Regress.	.482	.667	-.0012	.00085	-.068	-.238	.695		
	S. E.	.095	.245	.140	.135	.178	.035	.047	-.2212	87.6
	F	26.9**	7.38**	.72	.40	.15	46.5**	216.2**		
MS-D	Regress.	.555	-.073	-.0023	.0043	-1.024	-.065	.447		
	S. E.	.122	.328	.185	.179	.257	.064	.070	-1.1974	72.6
	F	20.8**	.05	1.58	.06	15.9**	1.03	40.2**		
HS-D	Regress.	.769	.300	-.0026	.0032	-1.127	-.364	.616		
	S. E.	.150	.413	.236	.227	.512	.172	.083	.3620	74.5
	F	26.2**	.52	1.26	2.04	4.84*	4.45*	54.9**		

^{1/}Regress.: Regression coefficient of a factor.
 S. E.: Standard error of regression.
 F: Variance ratio.
 **: Variance ratio exceeds 0.01 probability.
 *: Variance ratio exceeds 0.05 probability.

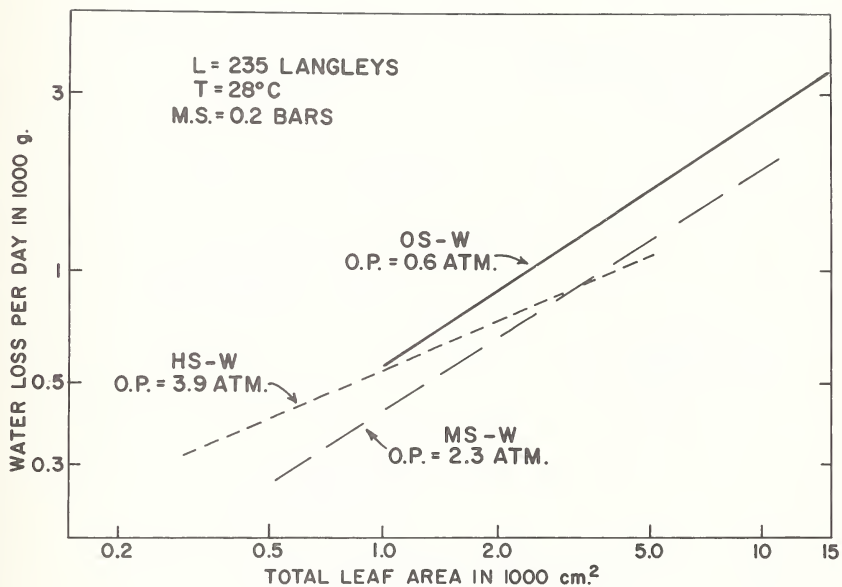


Figure 21

Water loss per day in the "wet" cultures in relation
to total leaf area

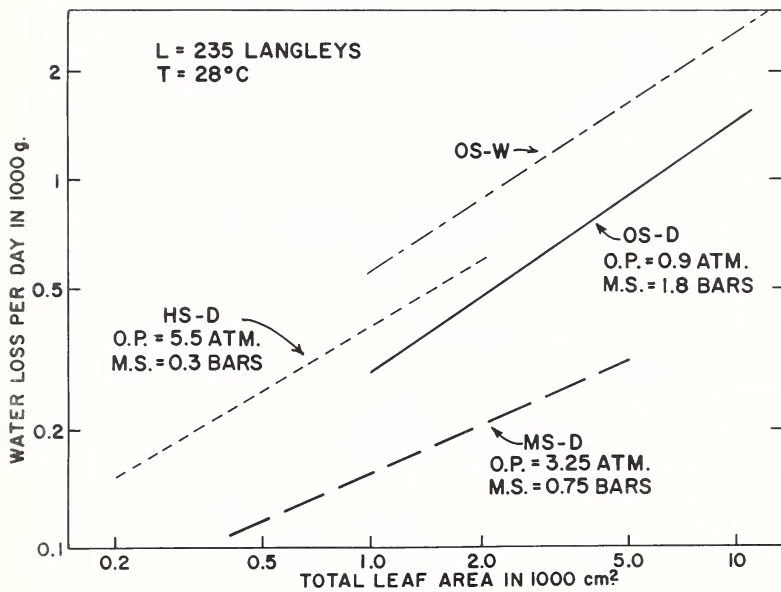


Figure 22

Water loss per day in the "dry" cultures in relation to total leaf area

may be associated with the fact that the F values of regression associated with leaf area were all very highly significant and imply that variations in leaf area accounted for a major portion in the variances in the data for evapotranspiration within the six treatments. This is as would be expected.

Although the regression lines in Figures 21 and 22 have very analagous slopes, there is appreciable displacement of their respective loci. The data for the "MS-D" plants were at a lower level than was anticipated and those for the "HS-D" plants were at a higher level. The loci of the curves in Figure 21 are reflected in the curves for the derivatives (equation [17]) presented in Figure 23. That is, the change in water loss with an increase of a cm^2 per day varied from about 400 mgs when the plants were small down to about 110-160 mgs for large plants. In other words, if water loss from the cultures is calculated in terms of leaf surface, it varied from 1.1 to 4.1 mm. per day. Milthorpe (21) reviews data showing transpirational losses varying from 1 to 12 mm. per day during the growing seasons of temperate regions. Thus the derived data presented herein are quite within expectancy.

The data in Table 14 illustrate the variability in change in water loss with change in area. As the plants become larger, the shading effects of one leaf over another affected interception of solar energy. Also, the larger plants completely shaded the soil surface and

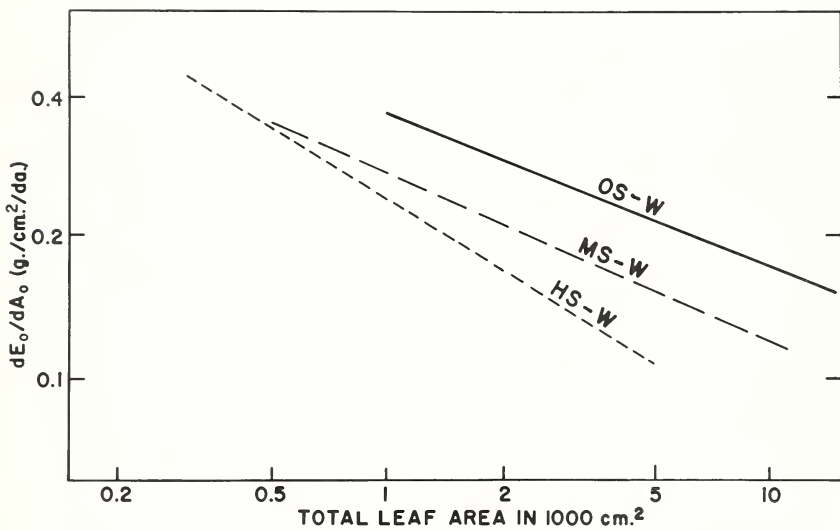


Figure 23

Rate of change in water loss per day in "wet" cultures in relation to total leaf area

Table 14

Increase in daily water loss per increase in leaf area
of 100 cm² within treatments

Leaf area increment cm ²	500 to 600	1000 to 1100	5000 to 5100	10,000 to 10,100
Treatment	gms.	gms.	gms.	gms.
OS-W	--	43	22	17
MS-W	34	27	15	12
HS-W	33	23	11	--
OS-D	--	20	16	10
MS-D	10	7	3	--
HS-D	35	16	--	--

undoubtedly curbed soil evaporation. In considering the data of Table 14, one must keep in mind that a solar radiation of 235 langleys per day was locked into the regression equations giving rise to Figures 21 and 22. The energy required to vaporize 1 gram of water at 28°C. is equivalent to about that of 580 langleys. Thus, the 235 calories/cm²/day should vaporize 400 mgs of water/cm²/day. Table 14 indicates this was exceeded (43 gms/100 cm²/day) by the "OS-W" plants when they were relatively small. There was some evaporation from the soil surface under small plants. Advective energy was also having an effect. For the most part, the data reveal the use of light energy in evapotranspiration was appreciably less than 100 per cent efficient.

The data for the "MS-D" and "HS-D" treatments appeared anomalous. It was appropriate, therefore, to ascertain whether these findings were also reflected in other data for water use efficiency. Figure 24 shows that the relation between total water loss per culture and total accumulated dry matter in the tops to be rather neat continuum. However, when these data were recalculated on the basis of water loss per gram of dry matter produced, and plotted against accumulated dry matter, an interesting relation appears, Figure 25. The "HS-D" cultures showed rather low water use efficiency, whereas those under "MS-D" revealed relatively high water use efficiency. This evaluation was independent of the regression analyses. The

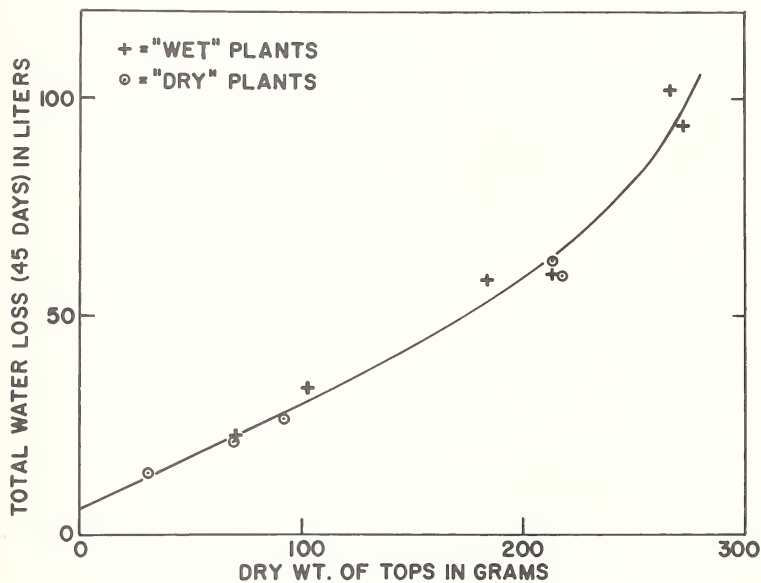


Figure 24

Total water loss in relation to dry weight accumulation
by individual plants

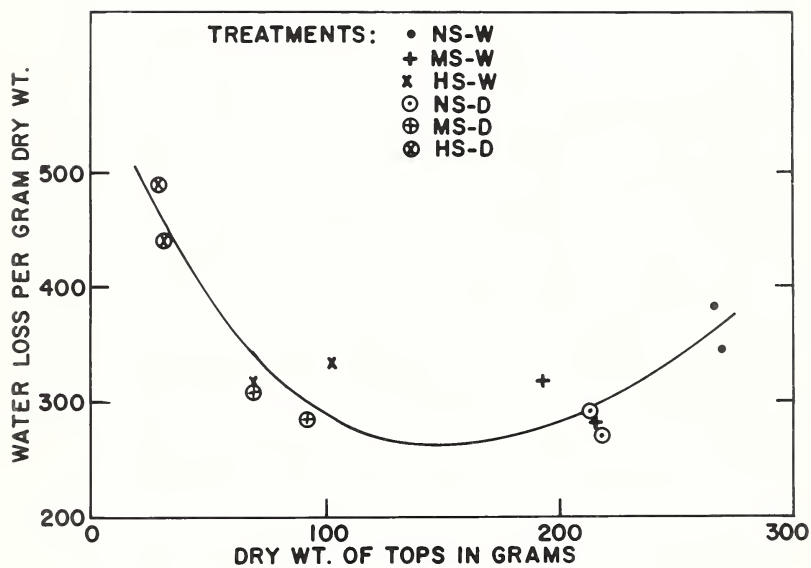


Figure 25

Water loss per gram dry weight in relation to dry matter accumulation

major portion of the curve to the right in Figure 25 shows that with a modicum of increase in soil moisture stress there is an increase in efficiency of water use; but that water stress due to high salinity is a quite different matter. Figures 22 and 25 provide indicate that elevated soil salinity may affect castor beans beyond that which may be accounted for by total soil moisture stress. The sodium chloride may well have had a specifically adverse effect.

Figure 26 shows the effect of change in matric suction upon the relation between water loss per day from a culture and increase in leaf area. The depressing effect of elevated matric suction on evapotranspiration is obvious and quite within expectation. As shown in Table 15, increasing matric suction from 0.3 to 5.0 bars was associated with a 50 per cent reduction in evapotranspiration per day at all levels of total leaf area. This finding corroborates comparable observations made under field conditions (1, 18).

The data in Table 13 associated with the light factor show that the regression coefficients between $\ln E$ and $\ln L$ were fairly consistent among the treatments; and that these regressions were all highly significant. It is far easier to reconcile these findings with reality than a situation in which the coefficients had shown wide diversity, or one in which the effect of increasing light energy had no significant effect on evapotranspiration. Nevertheless,

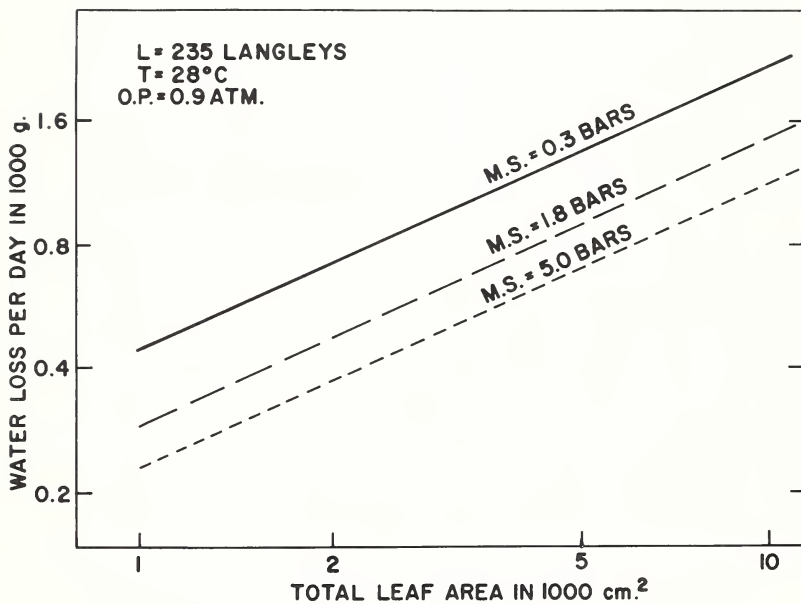


Figure 26

Water loss per day in relation to leaf area as affected by matric suction

Table 15

Increase in daily water loss per increase of 100 cm² in leaf area as affected by matric suction (OS-D plants)

Leaf area increment in cm ²	1000 to 1100	5000 to 5100	10,000 to 10,100
Matric suction in bars	gms.	gms.	gms.
0.3	31	20	16
1.8	20	16	10
5.0	15	10	8

one should note that the standard errors for the regression coefficients for light were much higher than the respective ones for leaf area.

Figures 27 and 28 set forth the relations between $\ln E$ and increasing $\ln L$ within the six treatments. A moderate level of increased salinity appreciably depressed water loss per increment of light; but the loci of the curves for the "high" level of salinity again show the apparently anomalous effect of this treatment, particularly under the "dry" regime. The derivatives for the curves in Figure 28 are shown in Figure 29; they indicate that rate of change in water loss with change in light was much less under "high" salinity than the "medium" level. This point may be more clearly brought out by reference to Table 16 showing the increment in water loss per cm^2 of leaf surface for an increment of light energy within the various treatments. Theoretically, an increase of 10 langleys of solar radiation per day should provide energy for an increase of $\frac{10}{585} \times 1000$ mgs of water; or 17.1 mgs of water per cm^2 surface. The values set forth in Table 16 are all somewhat below theoretical. This is not surprising. It is of interest that an increment of light energy incurred essentially the same increase in water loss among the first four treatments listed, with anomalous findings for the "MS-D" and "HS-D" treatments. The apparent lowering of effectiveness of an increment of 10 langleys

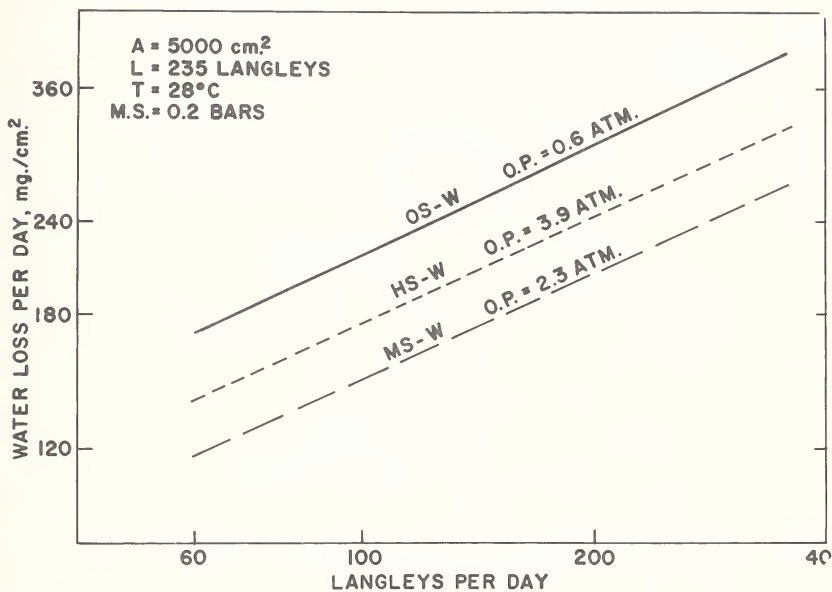


Figure 27

Water loss per day in relation to solar radiation as affected by salt level ("wet" cultures)

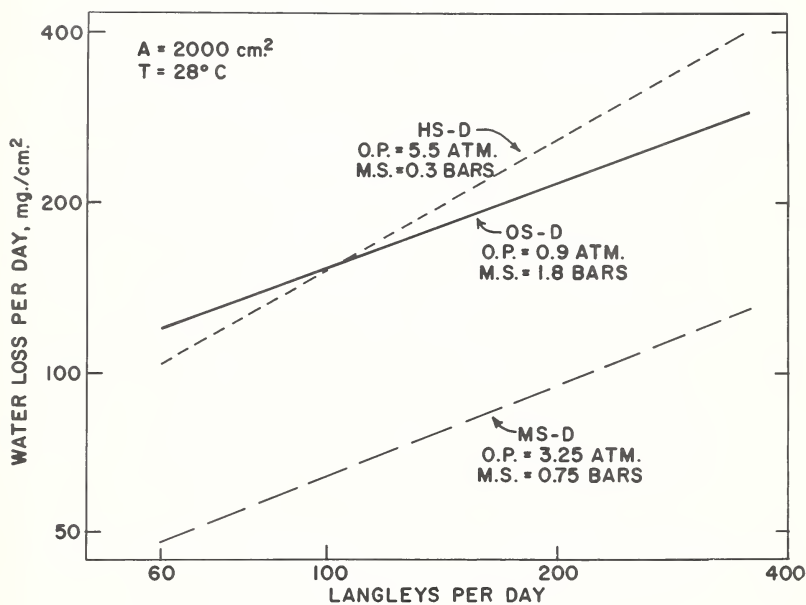


Figure 28

Water loss per day in relation to solar radiation as affected by salt level ("dry" cultures)

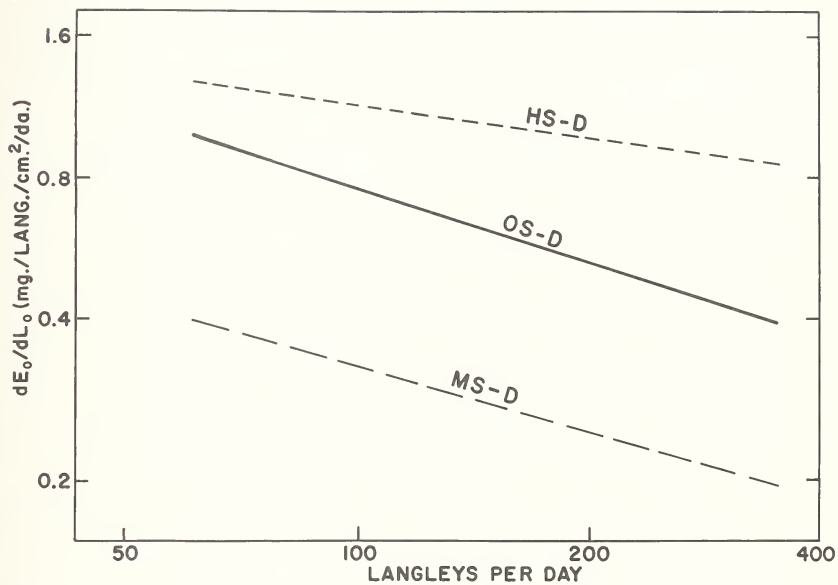


Figure 29

Rate of change in water loss per day in relation to solar radiation

Table 16

Increase in daily water loss per cm^2 of leaf surface for an increment in solar radiation at various light levels

Increment in solar radiation per day in langleys	90	235	350
	to 100	to 245	to 360
Treatment	mgs/ cm^2	mgs/ cm^2	mgs/ cm^2
OS-W	10.6	6.4	5.4
MS-W	8.2	5.2	4.3
HS-W	8.5	5.2	4.2
OS-D	7.8	4.9	3.9
MS-D	3.7	2.4	2.0
HS-D	12.1	9.7	8.9

at the higher levels of solar radiation are not readily explainable. This indication may be merely reflecting a mathematical constraint imposed by the derived relationship between logarithmic values.

The regression lines in Figure 30 show that an increase in the total leaf area of the plants effectively depressed the loci of the curves showing the relation between water loss per day and solar radiation for the "OS-W" or control cultures. This is more clearly set forth in Table 17 indicating the change in water loss per cm^2 of leaf surface for an increment in light energy at various levels of total leaf area. The derived values give evidence that efficiency of use of light energy in water vaporization decreased with the increased leaf shading that occurred with the larger values for total leaf area. It is of interest to note that increasing light energy from 90 to 100 langleys is an 11% increase, while that from 350 to 360 langleys is a 2.9% increase. Thus, in terms of relative increase in solar radiation, a one per cent increase in light at the higher light energies was associated with a higher increase in water loss/ cm^2 than at the low level of light. This suggests that relative increase in light may modulate the effect of actual increase light on water loss per unit area.

Figure 31 was derived from the equation for the "OS-D" cultures. It shows that increased matric suction markedly depressed the water loss per day related to increased solar

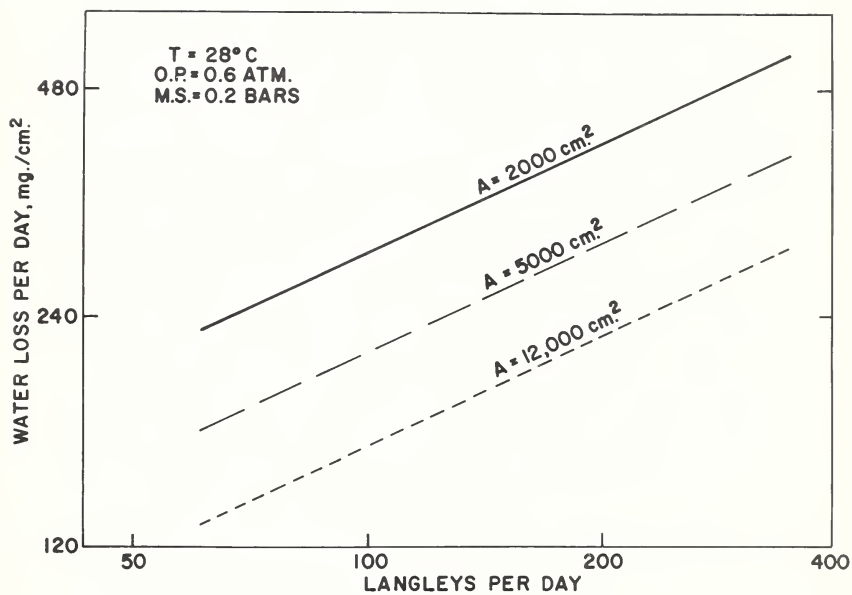


Figure 30

Water loss per day in relation to solar radiation as affected by leaf area

Table 17

Change in water loss per cm^2 per 10 langley increment of light at various levels of total leaf area

Increment of light in langleys	90 to 100	235 to 245	350 to 360
Total leaf area cm^2	mgs/cm^2	mgs/cm^2	mgs/cm^2
2000	14.4	8.7	7.2
5000	10.6	6.4	5.4
12,000	8.0	4.9	4.0
Relative	1.31/1% inc.	2.05/1% inc.	2.5/1% inc.

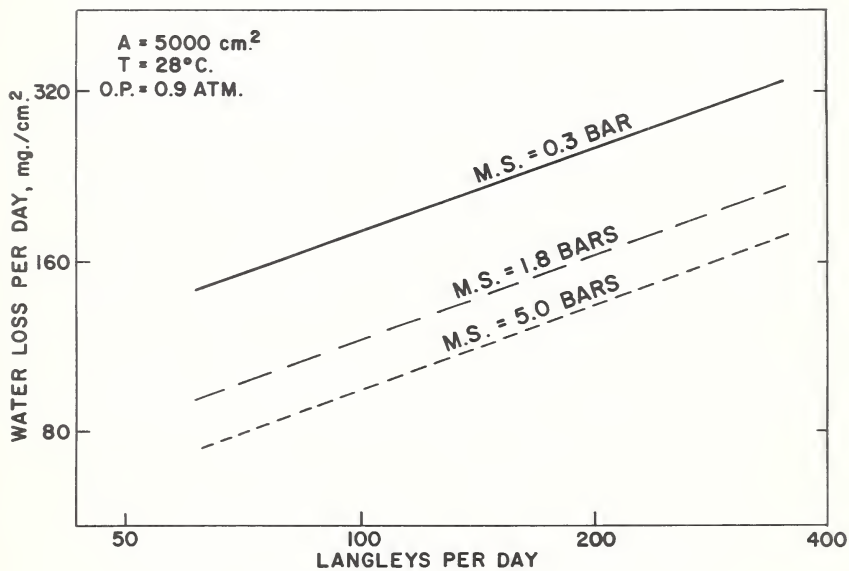


Figure 31

Water loss per day in relation to solar radiation as affected by matric suction

radiation. This effect is more explicitly set forth by the data in Table 18. Whereas increasing salinity in the "wet" cultures (Table 16) indicated little impact on change in water loss from a given increment of light, increasing matric suction had a marked effect. This observation again raised the suspicion that increasing moisture stress due to salinity may have a somewhat different effect than increasing stress due to matric suction.

Data in Table 13 show that the regression coefficient for the effect of air temperature on evapotranspiration were all relatively high - (0.834-0.870) - (and all highly significant) within the "wet" cultures. The unsalinized cultures in the "dry" series also produced a highly significant regression coefficient. The salinized cultures in the "dry" treatments revealed no significant relation between water loss and air temperature. It should be noted that the pertinent standard errors of regression were relatively high. The regressions are charted in Figures 32 and 33. Again, the anomalous loci of the "high" salt cultures are obvious. As shown in Table 19, the increment in water loss for a given increment in temperature changed little with increasing temperature within each of the "wet" treatments. In order to attain some indication of what potential water loss might have been for the increments in temperatures, potential

Table 18

Change in water loss per cm^2 of leaf surface as affected
by matric suction for a given increment in light

Light increment in langleys	90 to 100	235 to 245	350 to 360
Matric suction in bars	mgs/cm^2	mgs/cm^2	mgs/cm^2
0.3	9.0	5.5	4.6
1.8	5.9	3.7	2.9
5.0	4.6	2.9	2.3

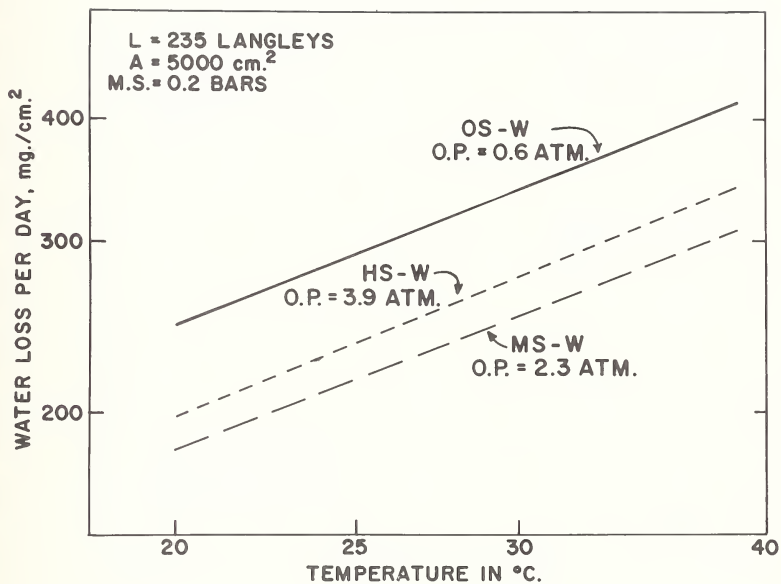


Figure 32

Water loss per day in relation to temperature as affected by salinity level ("wet" cultures)

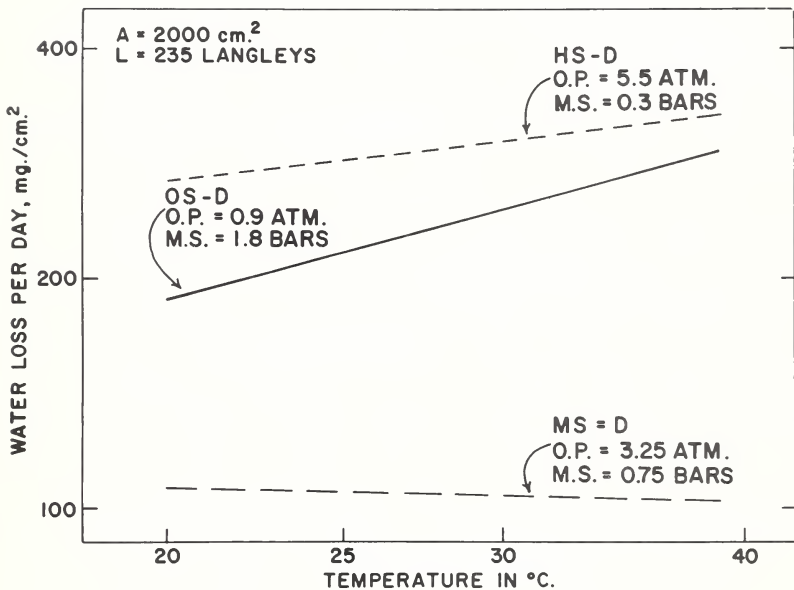


Figure 33

Water loss per day in relation to temperature as affected by salinity level ("dry" cultures)

Table 19

Change in water loss/cm² of leaf surface for an increment
in air temperature within the various treatments

Temperature increment in °C.	20 to 22	29 to 31	38 to 40
Treatment	mgs/cm ²	mgs/cm ²	mgs/cm ²
OS-W	20.7	19.6	18.9
MS-W	15.0	14.2	13.5
HS-W	17.0	16.3	15.7
OS-D	12.5	11.0	10.1
MS-D	-0.7	-0.5	-0.4
HS-D	7.8	6.1	5.0
Calculated potential evapotranspiration	39.8	43.5	46.4

evapotranspiration was calculated from Thornethwaite's formula (29), - a derivation that is largely dependent on air temperature. Actual calculation used temperature values in the heading of Table 19 and followed the procedure given by McGuinness and Bordne (20). The derived values converted to $\text{mgs/cm}^2/\text{day}$ are provided at the bottom of Table 19. They suggest that actual evapotranspiration from the cultures may be only one-half or less that of the calculated potential evapotranspiration. However, it must be emphasized that Thornethwaite's calculation is based on the mean daily temperature for a week or a month, whereas the temperature values used in the present study were the maximum temperatures prevailing for a two-hour period each day. Thus, the figures derived from Thornethwaite's formula and shown at the bottom of Table 19 should be considerably higher than those attained by use of equation [19].

It may be seen in Figure 34 that increasing total leaf area of the plants markedly depressed the loci of the regression curves relating water loss per day to increasing temperature. The increased shading from one leaf over another would have increased the cooling effect of evaporation. This effect is apparent in the values shown in Table 20. Increasing leaf area from 2000 to 12,000 cm^2 s nearly halved the change in rate of water loss for a 2-degree increment of temperature. It is also of interest

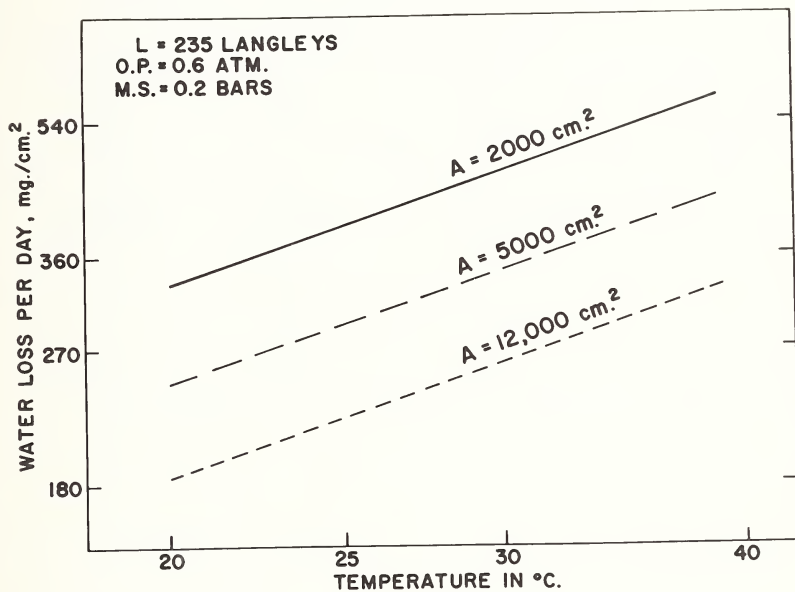


Figure 34

Water loss per day in relation to temperature as affected by total leaf area

Table 20

Change in water loss/cm² of leaf surface for an increment
of air temperature at various total leaf areas
on the "OS-W" plants

Leaf area per plant	20	29	38
	to	to	to
	22	31	40
	°C	°C	°C
cm ²	mgs/cm ²	mgs/cm ²	mgs/cm ²
2000	28.0	26.5	25.5
5000	20.7	19.6	18.9
12,000	15.5	14.8	14.2

that the value for this change (28.0) was about two-thirds the calculated value for potential evapotranspiration given at the bottom of Table 19.

The depressing effect of increasing soil moisture tension on the relation between air temperature and water loss per cm^2 is well illustrated by Figure 35. It corresponds rather exactly to observations made under field conditions (1). As shown in Table 21, increasing matric suction from 0.3 to 5.0 bars by drying of the soil incurred a halving of the change in water loss for an increment of air temperature.

A message comes through loud and clear from Table 13 that neither the readings for maximum daily humidity nor for minimum daily humidity had a relation to the recorded daily water losses from the experimental cultures. This is not to infer that moisture content of the atmosphere has no effect on the rate of water vaporization from a surface. Rather, within the present data there was a high degree of intercorrelation between solar radiation and relative humidity. That is, any impact that humidity may have had was completely overshadowed by the impact of light and temperature. The computer allocates maximum variance to the dominant independent variable when intercorrelation prevails.

It is of interest that Blaney (3) found it unnecessary to consider humidity when calculating consumptive use of water in irrigated areas; and that humidity is not involved in the Thornethwaite formula.

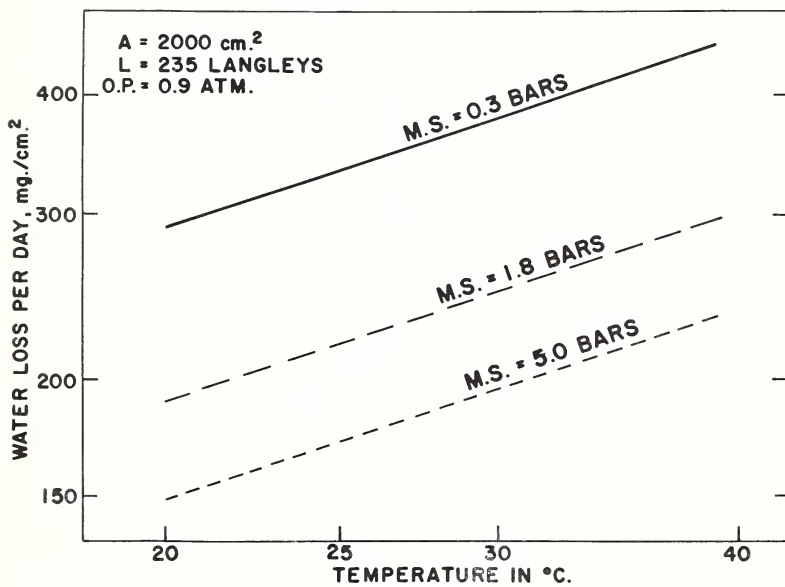


Figure 35

Water loss per day in relation to temperature as affected by matric suction

Table 21

The effect of increasing matric suction on the change in water loss per cm^2 with an increment of air temperature

Increment in temperature in °C.	20 to 22	29 to 31	38 to 40
Matric suction in bars	mgs/cm ²	mgs/cm ²	mgs/cm ²
0.3	19.0	16.9	15.5
1.8	12.5	11.0	10.1
5.0	9.7	8.6	7.9

The effects of salinity on water loss may not be adequately evaluated by reference to the values for osmotic pressure (O.P.) within the various treatments. Variations in O.P. within a treatment were relatively small as compared to differences between treatments that specifically involved increases in level of salt added to the soil (see Figure 11). Accordingly, the data for all salt treatments in the "wet" cultures were pooled; and all those in the "dry" cultures were pooled separately. The findings are shown in Table 22.

Within the "wet" cultures, the regression coefficients for area, light, and temperature in Table 22 are very near the average of the three separate values given in Table 13.

The value for the regression coefficient between $\ln E$ and $\ln P$ (-.125) appears to be relatively small, but it is a highly significant remover of variance. The range for P values in these data was small; it varied only from .55 to 5.1. The loci of the regression lines between $\ln E$ and $\ln P$ may change markedly, depending on the status on other environmental factors. This is shown in Figure 36. It is important to glance at the values presented to Table 23. The rate of change in water loss per cm^2 for 1 atmos. increment in osmotic pressure is shown to decrease rapidly as osmotic pressure of the soil solution increases. One could well have expected a decrease in the values at stipulated aerial environments, but the magnitude of the effect shown in Table 23 was greater than anticipated.

Table 22

Evaporation Coefficients (Pooled Data)

Treatment	Coef.	"Independent" Factors							K	R ² %
		Light	Temp.	H min	H max	O.P.	M.S.	Leaf area		
"Wet"	Regress ^{1/}	.472	.814	-.0010	.00015	-.125	-.025	.647		90.2
cultures	S.E.	.054	.146	.083	.081	.024	.040	.022	-.2971	
	F	76.8**	31.0**	1.52	.035	27.4**	.38	838.0**		
"Dry"	Regress	.622	.511	-.0011	.0016	-.378	-.224	.536		85.7
cultures	S.E.	.076	.210	.119	.117	.044	.021	.039	-.1520	
	F	67.4**	5.92*	.87	1.98	74.2**	116.6**	193.0**		
Pooled	Regress	.554	.740	-.0013	.0008	-.221	-.271	.663		88.4
cultures	S.E.	.049	.135	.076	.075	.024	.014	.021	-.5009	
	F	127.0**	30.0**	3.02	1.14	83.0**	356.0**	102.0**		
Pooled	Regress	.607	.649	-.0008	.0008	-.485	-.260	.617		89.7
cultures	S.E.	.047	.128	.072	.071	.039	.014	.020	-.1312	
with	F	169.0**	25.7**	1.23	1.24	155.0**	368.0**	920.0**		
quadratic										
effect of										
P and S										
2nd	Regress					-.243	-.030			
degree	S.E.					.029	.010			
effect	F					69.5**	8.5**			

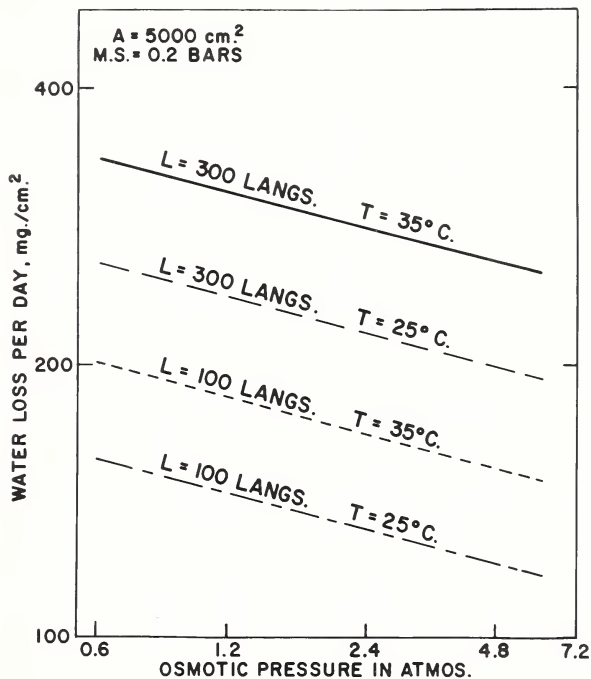


Figure 36

Water loss per day in relation to calculated osmotic pressure as affected by light and temperature ("wet" cultures)

Table 23

The effect of an increment in osmotic pressure on the change in water loss per cm^2 under stipulated aerial environments

O.P. Increment in atmos		0.5 to 1.5	2.5 to 3.5	4.5 to 5.5
Light in langleys	T ^o in C	mgs/cm ²	mgs/cm ²	mgs/cm ²
300	35	-45.2	-11.8	-6.6
300	25	-34.4	-9.0	-5.1
100	35	-27.0	-7.1	-3.8
100	25	-20.5	-5.3	-3.0

The statistics for the "dry" cultures in Table 22 were used in preparing Figure 37, since the data involved covered wide variability in values for matric suction (0.1 to 7 bars). It is important to note that the size of the regression coefficient associated with O.P. in the "dry" cultures was three times the magnitude of that found in the "wet" cultures; that is, there was a much wider diversity in water loss values associated with the "dry" series than the others. It is possible that much of the effect due to water depletion of the soil is appearing as increased osmotic pressure of the soil solution as well as increased matric suction.

It is very evident in Figure 37 that increasing matric suction depresses the loci of the curves relating water loss and O.P., with a major change taking place between 0.1 and 0.5 bars of matric suction. This is shown in Table 24. The values for increase in water loss for an increment in O.P. from 0.5 to 1.5 atmos appear to be exceedingly high in Table 24. They may be a reflection of the mathematical constraints of the linear regression between logarithmic values rather than actuality.

To test this latter, all data were pooled for a multiple regression analysis (Table 22). The constants with all regressions linear are shown in the third tier of values. The pooled data were also programmed so that the relation between $\ln E$ and $\ln P$; and between $\ln E$ and $\ln S$ were treated as parabolic functions. Thus, equation

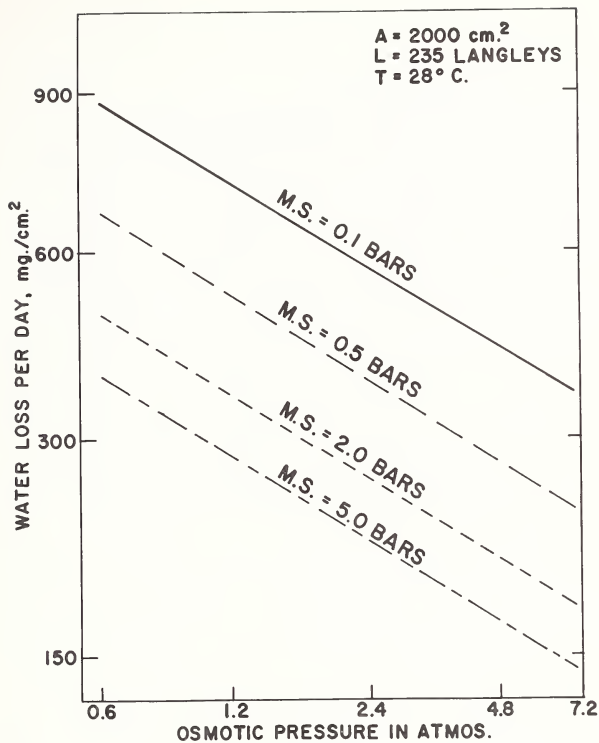


Figure 37

Water loss per day in relation to calculated osmotic pressure as affected by matric suction ("dry" cultures)

Table 24

Change in water loss per increment in O.P.

Increment in O.P. matric suction	0.5 to 1.5 atmos.	2.5 to 3.5 atmos.	4.5 to 5.5 atmos.
bars	mgs/cm ²	mgs/cm ²	mgs/cm ²
0.1	-318.9	-61.0	-29.9
0.5	-212.5	-42.6	-20.4
2.0	-163.1	-31.2	-15.3
5.0	-132.8	-25.4	-12.5

[19] became:

$$\ln E = \ln K + a \ln L + b \ln T + c \ln H_n + d \ln H_x \\ + e \ln P + f(\ln P)^2 + g \ln S = h(\ln S)^2 + i \ln A \quad [20].$$

The values in Table 22 show that the regressions for the second degree effect for both O.P. and M.S. were highly significant, even though the latter had a value of only -.030.

Obviously, the parabolic functions in Figure 38 tell quite a different story than Figures 36 and 37. The curves in Figure 38 go through a maximum of 1 atmos O.P. with the slope changing from positive to negative at that point. Thus, Table 25 shows the change in water loss per cm^2 with an increment in O.P. from 0.5 to 1.5 atmos. to be positive values. Although these are undoubtedly nearer reality than the comparable ones shown in the first column of Table 24, an experienced observer would be inclined to suggest that the change in water loss per cm^2 for the one atmos. increment at the low levels of O.P. should be about zero. Other values in Table 25 appear to be nearer reality than analogous ones in Table 24.

There is no question that it was essential to treat the relation between $\ln E$ and $\ln P$ as a curvilinear effect.

The curvilinear relationship between $\ln E$ and $\ln S$ as modified by O.P. and temperature is shown in Figure 39. These curves did not turn out as anticipated. Since there was some indication that the regression coefficients

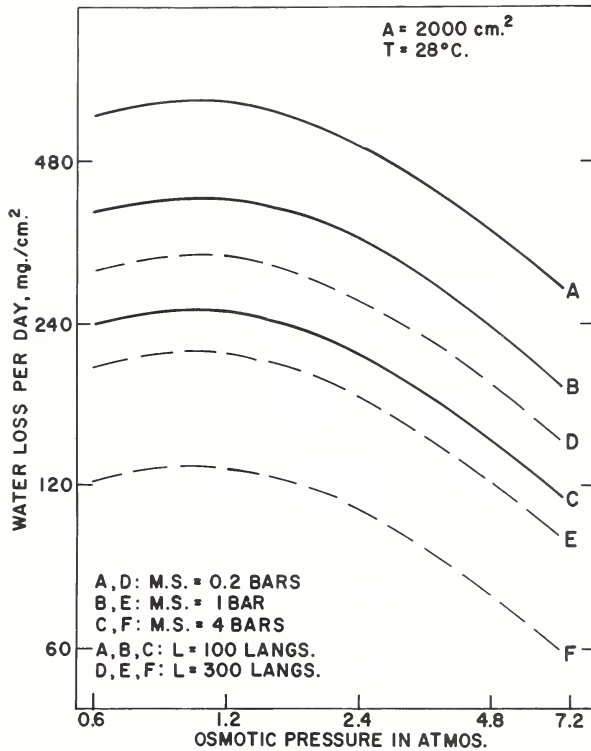


Figure 38

Water loss per day in relation to calculated osmotic pressure after conversion to a linear scale

Table 25

The effect of different levels of light and matric suction on the change in water loss per cm^2 for an increment in osmotic pressure under a parabolic relationship

Increments in O.P. Am.		0.5 to 1.5	2.5 to 3.5	4.5 to 5.5
Light in langleys	Matric suction in bars	mgs/cm ²	mgs/cm ²	mgs/cm ²
300	0.2	+43.7	-82.3	-51.9
300	1.0	+28.8	-54.4	-33.3
300	4.0	+17.8	-33.6	-21.2
100	0.2	+22.4	-42.2	-26.6
100	1.0	+14.9	-27.9	-17.6
100	4.0	+ 9.2	-17.3	-10.9

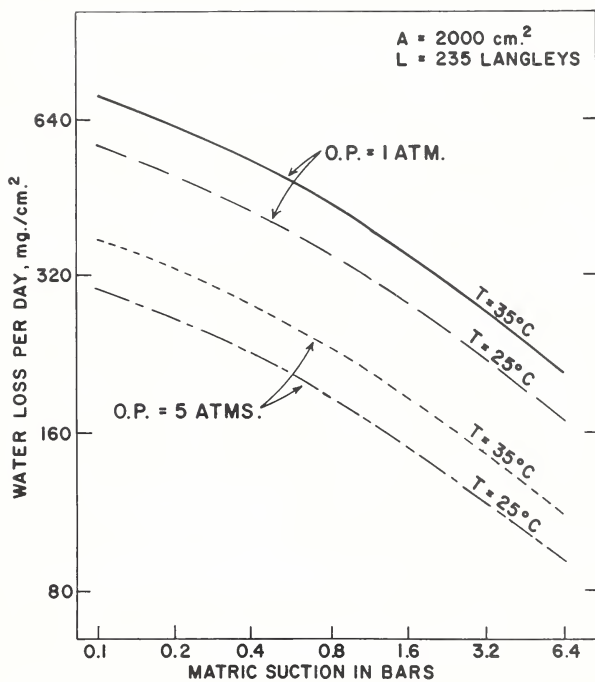


Figure 39

Water loss per day in relation to matric suction after conversion to a linear scale

between $\ln E$ and $\ln S$ to be positive in the "wet" cultures (Table 13), one might have anticipated that the curves in Figure 40 would have passed through a maximum of 0.2 - 0.25 bars. Thus, these curves should be looked on as an indication of the relationship and not the precise trend. That is, one would be inclined to question the magnitude of the values for change in water loss per increment of M.S. at the low level of matric suction. However, it is essential to keep in mind Gardner's (9) findings showing the tremendous change in evaporation from a soil surface between 0.2 and 0.5 bars of matric suction. Hence, the data in Table 26 may well be fairly accurate reflection of the effect shown by Gardner.

Equation [19] as modified to include the quadratic effect of O.P. and M.S. (Table 22) was differentiated to determine $\frac{dE_o}{dP_o}$ and $\frac{dE_o}{dP_o}$. In each of the respective cases, O.P. or M.E. were locked into equation [19] at values that would be associated with nearly maximum evapotranspiration. The results appear in Figure 40. The loci of the curves below 1.5 atmos. of soil moisture stress are quite divergent, and appear to be displaying effects heretofore discussed. The remaining portions of the curve lie within the same "ballpark," but the displacement between them again suggests the elevated salinity in the soil has an effect on rate of water loss that is beyond that which may be fully accounted for by decreasing free energy of the soil water.

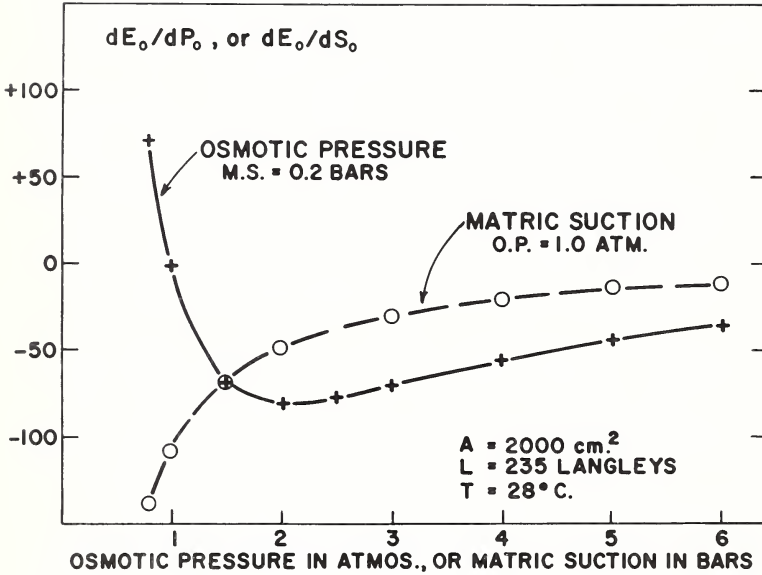


Figure 40

Rate of change in water loss per day in relation to
osmotic pressure or matric suction

Table 26

Change in rate of water loss per unit increment in matric suction as modified by O.P. and temperature

Increment in matric suction in bars		0.2 to 1.2	2.2 to 3.2	4.2 to 5.2
O.P.	Temp.			
Atm.	°C	mgs/cm ²	mgs/cm ²	mgs/cm ²
1	25	-187.7	-32.4	-16.2
1	35	-232.2	-40.3	-20.2
5	25	- 99.4	-17.2	- 8.6
5	35	-172.0	-29.5	-14.9

Table 27 presents a recapitulation of the findings set forth in this section. The range of values developed by this empirical approach are reasonably close to those that might have been anticipated from a rationalization of theoretical considerations.

It is always advisable to gain an indication of how well the calculated values from a multiple regression analysis agree with the observed values. The calculated water loss data was attained by use of equation [19] and the constants presented in Table 13. Figure 41 shows the findings for the "OS-W" treatment. If the calculated values had been identical with the observed data, they would have all fallen on the 45° line. Obviously, there was dispersion. The standard error of estimate was 0.1437 for the calculated values of $\ln E$. With anti-logarithmic transformation, there is greater deviation for the lower limit of SE than the upper limit. Theoretically, two-thirds of the coordinated points should have fallen within the confines of the S.E. lines. This was close to actuality.

Prediction was not as good as one might have anticipated, but it is essential to keep in mind that the data accrued from the daily weighing of the oil drums of soil with varying plant weights constituted something less than ultimate precision in data acquisition. Other treatments were associated with even less concurrence of calculated values with those measured. The respective standard

Table 27

Range in values for water loss per unit area of leaf surface associated with a unit increment of a given environmental factor

Factor ^{1/}	Unit of change	Range in water loss mgs/cm ²
Area	1 cm ²	100 to 400
Light	1 langley	0.4 to 1.2
Temp.	1°C	2 to 10
O.P.	1 atmos	0 to -50
S.M.	1 bar	-10 to -100

^{1/}Other factors than the one specified considered to be at the following levels:

Leaf area = 2000 cms²

Light = 235 langleys

Temp. = 28°C

O.P. = 1 atmos.

M.S. = 0.2 bars

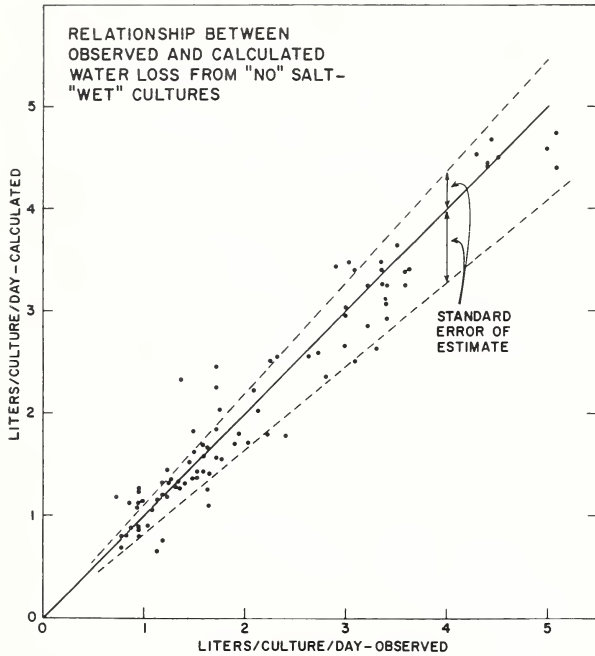


Figure 41

Relation between observed and calculated values derived by
equation [13]

errors of estimate were: "OS-W," 0.1437; "MS-W," 0.2066; "HS-W," 0.2761; "OS-D," 0.2210; "MS-D," 0.2931; and "HS-D," 0.3706.

Even though the R^2 values in Tables 13 and 22 show that a high proportion of the variance among values for $\ln E$ was accounted for by the respective treatments, one must conclude that equation [19] is not wholly adequate as a predictive tool.

Leaf Elongation

Use of a logistic equation. The conventional approach to evaluating plant growth that follows a logistic trend involves the use of equation [1]. This function carries the constraint that the trend of the curve to the right of the inflection point be a mirror image of the trend to the left of that point. Said point occurs at the value of the independent variable where the derivative of equation [1] goes through a maximum. The "b" values in this equation are rate constants; i.e., they are indices of the comparative rates of growth for comparable sets of measurements. One might superficially deduce that variations in magnitude of "b" merely indicates that large plants grow faster than small plants. This is not necessarily the case.

Daily measurements of leaf elongation such as shown in Figures 14, 16, 17, and 18 were accrued on about 125 leaves. The value of "b" was determined by use of equation [2] as transformed from [1] for selected leaves in each treatment. The findings are shown in Figures 42, 43, 44, 45, 46, and 47.^{1/}

On a given plant, there was wide variation in total length of leaves emanating from successive nodes up the stem (see Figure 14); yet, there was little variation in the magnitudes of "b" on a given plant. Soil treatments

^{1/}In equation [2], b is a positive value with a negative algebraic sign. The negative sign is attached in the specified figures since the slopes are obviously negative.

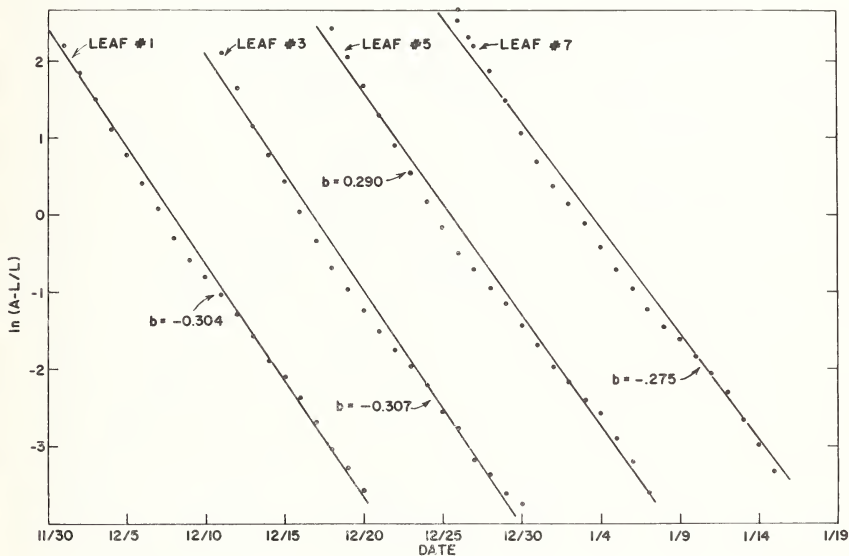


Figure 42

Leaf elongation expressed as $\ln\left(\frac{A-L}{L}\right)$ in relation to time
on the "0" salt-wet treatment

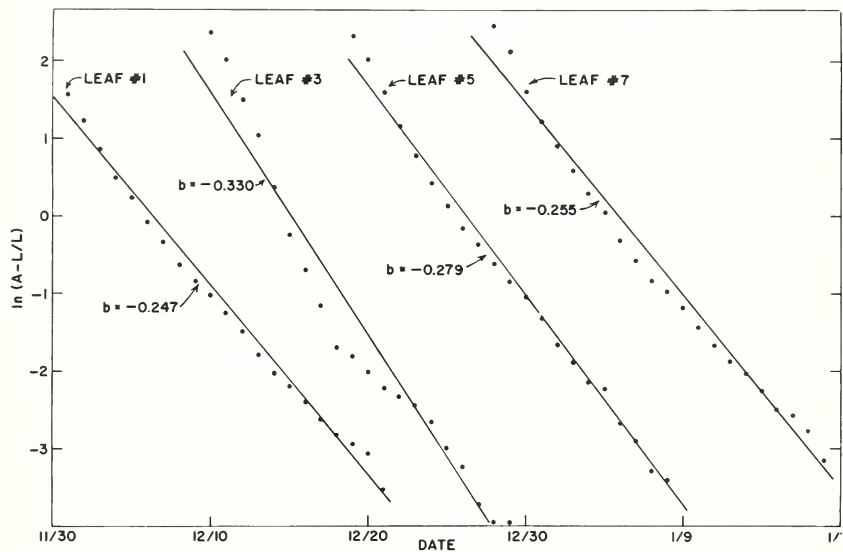


Figure 43

Leaf elongation expressed as $\ln\left(\frac{A-L}{L}\right)$ in relation to time on the "med." salt-wet treatment

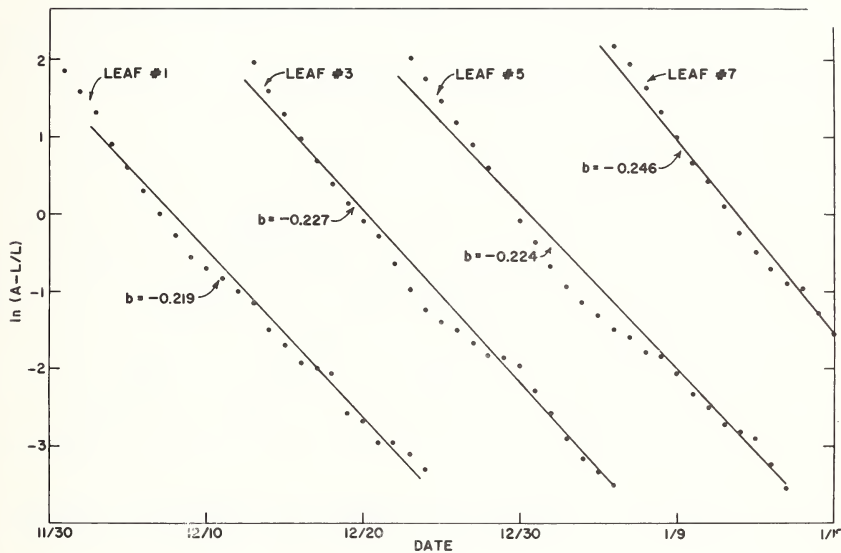


Figure 44

Leaf elongation expressed as $\ln\left(\frac{A-L}{L}\right)$ in relation to time
on the "high" salt-wet treatment

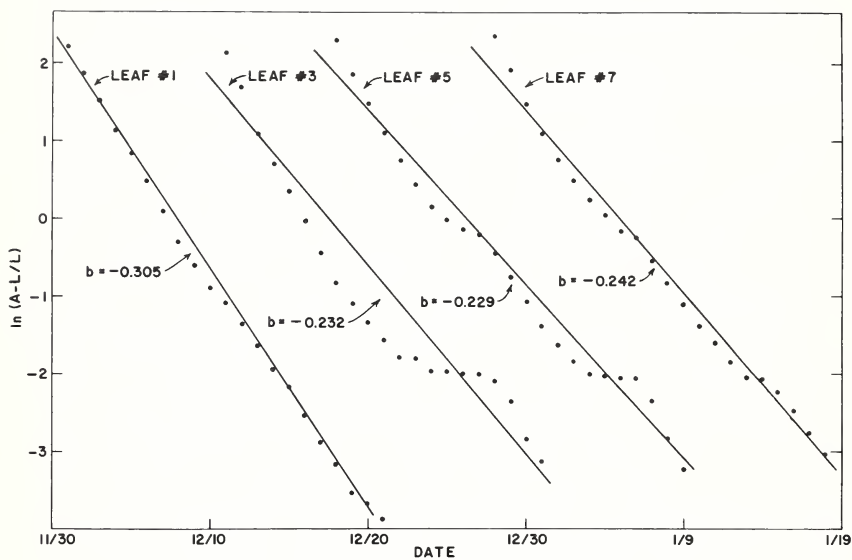


Figure 45

Leaf elongation expressed as $\ln\left(\frac{A-L}{L}\right)$ in relation to time
on the "0" salt-dry treatment

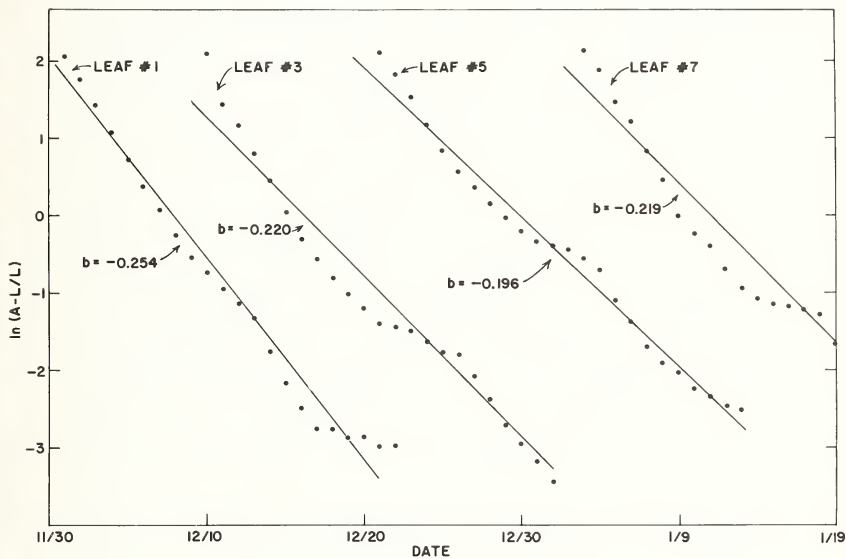


Figure 46

Leaf elongation expressed as $\ln\left(\frac{A-L}{L}\right)$ in relation to time on the "med." salt-dry treatment

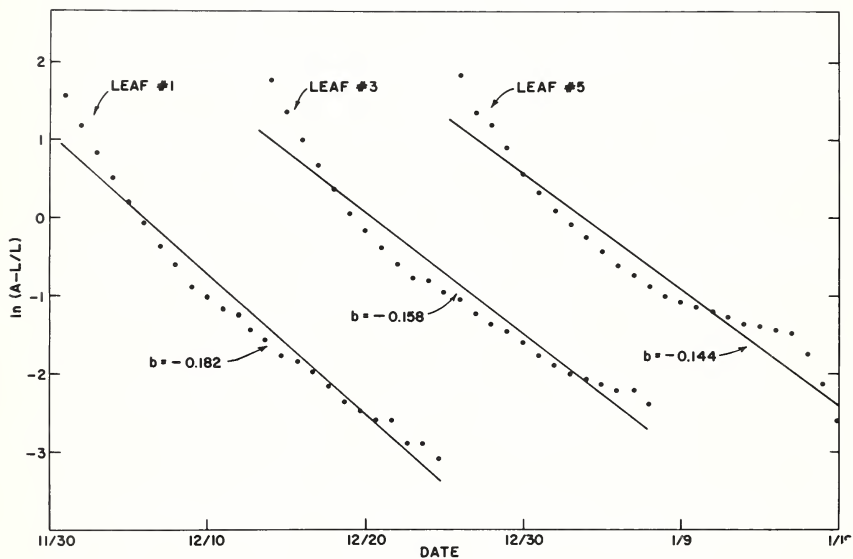


Figure 47

Leaf elongation expressed as $\ln\left(\frac{A-L}{L}\right)$ in relation to time
on the "high" salt-dry treatment

very definitely affected the magnitude of "b." This point is emphasized by the analysis of variance of these "b" values in Table 28. Water regimes and salt levels in the cultures had a tremendous impact on changing the value of "b"; but there was no interaction between the effects of these two environmental stresses. Leaf position on the plants, regardless of the great variation in size of leaves on a given plant, had no significant effect on the index of growth rate, - "b." It is not clear as to how changes in the size of "b" may be related to changes in the levels of anabolism or catabolism analogous to von Bertalanffy's (2) work with growth of animals. It may be that the findings in Tables 28 and 29 are merely reflecting the degree to which water deficits prevailed within the plants due to soil treatments. The changes in mean value for "b" in Table 29 are all consistent with changes in average level of water deficit within the plants that should take place as a consequence of increased soil moisture stress within the cultures.

A primary purpose of this study was to ascertain the extent to which daily variations from the general trend in growth response were associated with daily variations in the intensity of the various environmental stresses. It is immediately obvious that the linear regressions in Figures 42 through 47 do not adequately represent the actual trend. The points for the recorded data show that to even

Table 28

Analysis of variance of "b" values in Figures 42-47

Source of variance	Degrees of freedom	Mean square variance	F Value
Water regimes	1	.018816	57**
Salt levels	2	.013298	40**
Water X salt	2	.000406	1.2
Leaf position	3	.000829	2.5
Water X leaf level	3	.001659	5.0
Salt X leaf level	6	.000421	1.3
Residual (error) ^{1/}	5	.000330	

**Significant at well beyond the 1% level of probability (F = 16).

^{1/}Corrected for the calculated value (missing plot) used for leaf #7 in Figure 47.

Table 29

Mean values for "b" associated with cultural treatments

	"Wet" cultures	"Dry" cultures	Average
No salt	.294	.252	.273
Med. salt	.278	.222	.250
High salt	.229	.158	.194
Average	.267	.211	.239

approach the actual trend, a cubic function of t as given in equation [3] and as transformed to equation [4] would be essential.

It would be quite superfluous to report all the statistics accrued from the analysis of data on the 125 different leaves that were measured. Table 30 presents the mean values for each constant for the measured leaves on each plant together with the coefficients of variability.

First of all, one must recognize that the regression coefficients in Table 30 are without physiological significance. The constant "a" merely shows the intercept with the dependent variable at zero time; "b," the slope of regression line at about zero time; and "c" and "d" indicate degree of deviation from linearity over the course of the curve. Obviously, resorting to a cubic function to express the trend with time would have been futile if such a step did provide an improved expression of the observed growth of the leaves. Analysis of variance was used to test the effect of expressing time as a cubic function. An example of this test is shown in Table 31. In every case, the cubic effect was found to be a highly significant remover of variance beyond that associated with linearity.

The effect of treatment on the mean values of the constants are better shown in Table 32. Salinity level had a significant effect in modifying the mean value of these constants, but water regime was essentially without influence.

Table 30

Mean of coefficients derived from individual leaves for the cubic function of time (Equation [4]) and the coefficients of variability of these means

Treatment	Culture No.	Statistic	Constant			
			a	b	c	d
OS-W	6	Mean	2.98	-.447	.0122	-.000250
		C.V. in %	5.7	17.9	74.0	127.0
	12	Mean	3.01	-.450	.00993	-.000205
		C.V. in %	6.6	32.0	121.0	168.0
MS-W	3	Mean	2.92	-.530	.0216	-.000506
		C.V. in %	11.3	36.0	51.0	56.0
	11	Mean	2.91	-.457	.0130	-.000231
		C.V. in %	9.0	11.3	37.0	64.0
HS-W	4	Mean	2.41	-.389	.0113	-.000198
		C.V. in %	7.3	18.0	57.0	80.0
	7	Mean	2.46	-.406	.0128	-.000243
		C.V. in %	4.5	6.7	30.0	48.0
OS-D	5	Mean	2.80	-.455	.0130	-.000219
		C.V. in %	5.8	22.0	112.0	186.0
	9	Mean	3.15	-.498	.0165	-.000317
		C.V. in %	6.7	24.0	64.0	81.0
MS-D	1	Mean	2.61	-.477	.0193	-.000356
		C.V. in %	11.0	22.0	57.0	84.0
	10	Mean	2.66	-.500	.0225	-.000480
		C.V. in %	8.5	24.0	44.0	61.0
HS-D	2	Mean	2.23	-.413	.0158	-.000298
		C.V. in %	8.4	10.4	20.0	31.0
	8	Mean	2.13	-.389	.0144	-.000287
		C.V. in %	14.0	37.0	82.0	88.0

Table 31

Variance in values of $\ln \frac{S-L}{L}$ removed by use of a cubic function of time (Plant 6 - Leaf 5)

Effect	Degrees of freedom	Mean square	F
Linear	1	63.249	19000
Cubic	2	.2305	69**
Error	17	.00333	

**Significant at a probability beyond % (F at .01 = 6.1.

Table 32

Mean values for the constants in the cubic function of time
(Equation [4] as affected by treatment)

Treatment	a	b	c	d
OS-W	3.00	-.448	.0111	-.000227
MS-W	2.91	-.493	.0173	-.000368
HS-W	2.43	-.397	.0120	-.000220
OS-D	2.97	-.476	.0147	-.000268
MS-D	2.63	-.488	.0209	-.000418
HS-D	2.18	-.401	.0151	-.000292
OS	2.98	-.462	.0129	-.000247
MS	2.77	-.490	.0191	-.000393
HS	2.30	-.399	.0135	-.000256
W	2.78	-.446	.0135	-.000272
D	2.68	-.455	.0169	-.000326

Actually there is little to be gained by detailed consideration of the mass curves and their derived constants for the growth of the leaves. The day-to-day increments in growth as modified by environmental stresses was the actual objective of this study.

Values for calculated daily increments could be attained by use of equation [5]. As shown by Figure 48, values for $\Delta L/\Delta t$ fall on precisely the same curve as those for dL/dt ; so the former were used in relating to environmental stresses. Designating ΔL to represent actual elongation on a given day and $\Delta L'$ as the calculated value, then $\Delta L/\Delta L'$ should be an index of the leaf-growing potential of environmental conditions prevailing on a given day. The results of attempting to relate $\Delta L/\Delta L'$ to records on the daily status of the environment were disappointing.

Reference to Figure 49 provides a good insight as to the basis for the aforementioned disappointment. The derivatives of equation [3] using the calculated constants are plotted as the curves in Figure 49 for three of the leaves on plant #6. The actual increments in growth for a given leaf are also plotted as points. An anomaly that prevailed through the data for leaf elongation is illustrated. In almost every case, the derived curve did not, adequately: a, indicate the rapid increase in rate of elongation over the first five days; b, indicate the maximum growth rate attained; and c, indicate the rapid decrease in rate of growth following a few days at maximum rate.

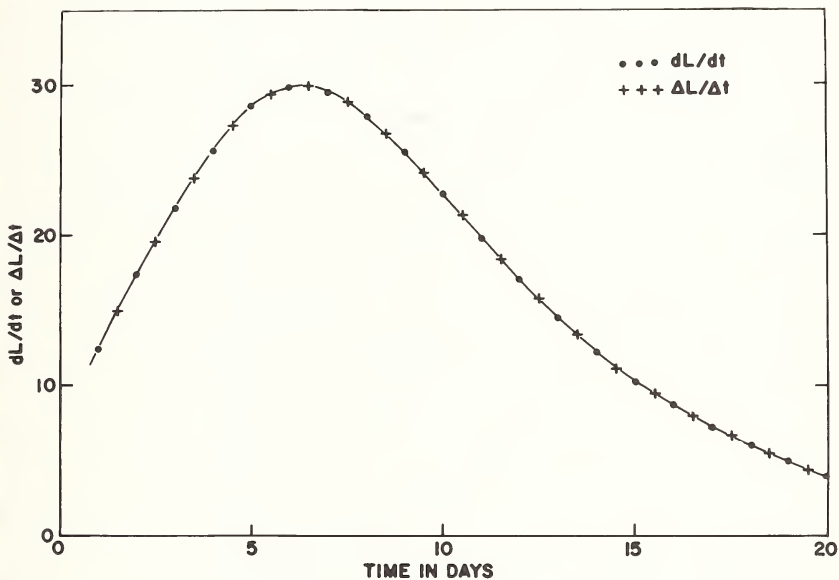


Figure 48

Comparison of the trend in calculated values in dL/dt by use of equation [5], in relation to derived values for $\Delta L/\Delta t$

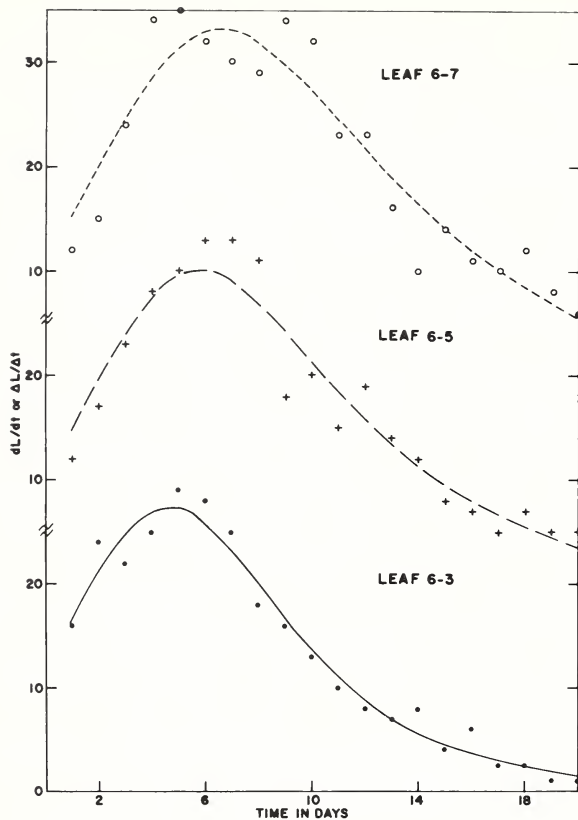


Figure 49

Calculated values for $\Delta L/\Delta t$ for leaves (the curves) on plant No. 6, in relation to actual values

In other words, the curves in Figures 13, 15, 16, and 17 derived by use of equation [3], and those in Figure 49 from equation [5] appear to be good fits of the data; but they proved to be quite inadequate for the purposes of this study.

One is led to the conclusion that fitting logistic curves to data on leaf elongation serves far better as an intellectual exercise than as an insight into plant performance.

Use of Richards' "m" factor. Relatively few data on plant growth having a sigmoid trend may be exactly fitted by a completely symmetrical logistic curve. In such a curve, the inflection point, I, in the growth measurements occurs at one-half the value of the asymptote, A, for the ultimate in growth measurement; i.e., $I = \frac{A}{2}$. The trend of the curve above the inflection point is a mirror image of that below; and the derivative of the logistic evolves a fully symmetrical "normal" curve typical of populations studies with maximum in the normal curve occurring at the time of the inflection in the logistic curve. As illustrated by Figures 48 and 49, the data from this study on leaf growth in no instance exactly fitted a symmetrical logistic.^{1/} Thus, the derivatives of the sigmoid trends provided curves analogous to those of populations with skewed distributions.

Richards (23) recognized that such asymmetry is usually the case in the trend of measurements on a growth response. Even though an asymmetric logistic using a cubic function of time will fairly well express mathematically the observed data, the derived coefficients for time in such a function have no physiological meaning.

Richards adapted von Bertalanffy's (2) "m" factor as a mathematical adjustment of data so that it would fit a symmetrical sigmoid curve. He emphasized that his (Richards') use of "m" makes it a strictly empirical

^{1/}The derivative of such a logistic provides a curve with the symmetry of a normal curve.

factor without the metabolic implications proposed by von Bertalanffy.

In Richards' usage, "m" is defined as being of such magnitude that

$$\frac{I}{A} = m^{1/(1-m)} \quad [21]$$

where, I = growth measurement at the inflection point, and A = growth measurement at the ultimate. Since I/A has a value of 0.5 in a symmetrical sigmoid, it becomes obvious that "m" has a value 2 when complete symmetry prevails. As "m" deviates from a value of 2, it is indicative of the degree of deviation from symmetry. The value of "m" is not directly derivable from equation [21]. Richards recommends the procedure of selecting an arbitrary set of values for "m," calculating corresponding values for $m^{1/(1-m)}$, drawing a curve relating the two, and using the curve to find desired values of "m" associated with values of $m^{1/(1-m)}$ derived by equation [21]. In this study, the value of I for each leaf was determined as the length of the leaf at the time when dL/dt of equation [5] attained a maximum.

Dr. Richards points out that a comprehensive function of growth, G, may be expressed as:

$$G^{1-m} = A^{1-m}(1 + be^{-kt}) \quad [22]$$

where A is the asymptote of growth, t is time, e the base of naperian logarithm, and b and k are constants.

If "m" has a value of 2 as noted above, equation [22] becomes:

$$G^{-1} = A^{-1}(1 + be^{-kt}) \quad [23]$$

or
$$G = \frac{A}{1 + be^{-kt}} \quad [24]$$

which is identical with equation [1] for a symmetrical logistic. For values of "m" exceeding unity, equation [24] may be expressed

$$G^{m-1} = \frac{A^{m-1}}{1 + be^{-kt}} \quad [25]$$

When m is less than unity, equation [22] is adjusted by raising all entities in the equation by a power of -1. Thus, equation [22] becomes:

$$G^{1-m} = \frac{A^{1-m}}{1 + be^{-kt}} \quad [26]$$

In deriving constants b and k, equation [26] may be expressed as:

$$\ln\left(\frac{A^{1-m} - G^{1-m}}{G^{1-m}}\right) = \ln b - kt \quad [27]$$

and equation [25] as:

$$\ln\left(\frac{A^{m-1} - G^{m-1}}{G^{m-1}}\right) = \ln b - kt \quad [28]$$

The constant, b, has no physiological meaning. It merely indicates the value of the ordinal intercept when the scale for time is at zero. The constant, k, shows the rate of change in the growth function with time, but its interpretation is complicated when different values of "m" are involved.

A bit of illustration may be advisable. Curve I in Figure 50 is a hypothetical growth curve in sigmoid form that is completely symmetrical. The constant "m" has a value of 2. Curve II is an asymmetric logistic typical of the growth responses found in this study. For curve II, m has a value of 0.92. In Figure 51, showing the rate trends of the curves in Figure 50, Curve I is a "normal" curve that is symmetric, whereas Curve II is skewed. As mentioned earlier, Richards recommended use of the "m" factor in equation [22] to adjust for inherent skewness.

Richards points out that the curves in Figure 51 may be expressed by the equation:

$$dG/dt = \frac{-kA^m e^{-kt}}{1-m} (1 + e^{-kt})^{m/(1-m)} \quad [29]$$

The form of the curves in Figure 51 is determined by m, but the maximum also depends on "A" and "k." The area under these curves is given by Richards as:

$$G = A \int \frac{kG}{1-m} \left(\frac{A}{G}\right)^{1-m} - 1 \quad dG = A^2 k / (2m + 2) \quad [30]$$

$$G = 0$$

Hence, the mean height of these curves; i.e., the mean growth rate over the growth period is gained by dividing equation [30] by A. That is, $\frac{Ak}{2m + 2}$ is the weighted mean elongation rate per day. If growth were measured in units so that the final length of the leaf, A, was unity and the rate plotted against the adjusted values of G, then the area under the curves becomes: $\frac{k}{2m + 2}$, which is the proportional average rate over the whole length from 0 to 1. It is important to

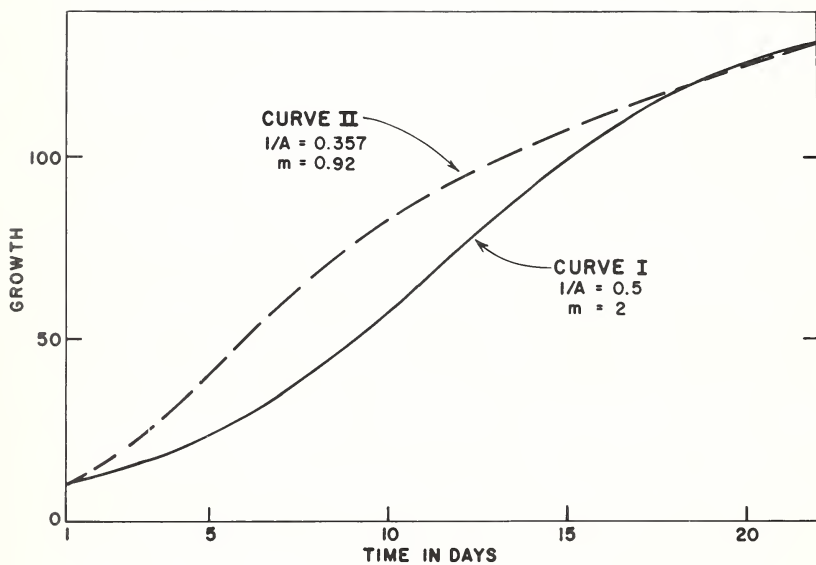


Figure 50

Loci of two hypothetical growth curves of the logistic form

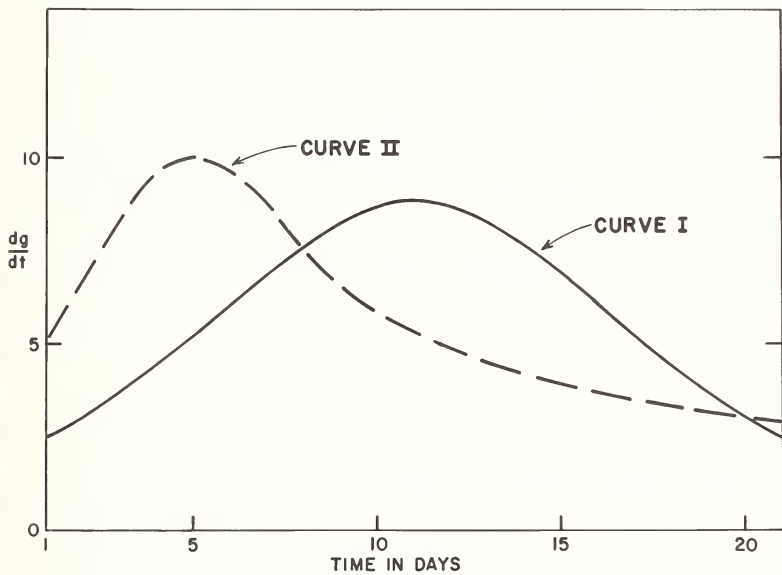


Figure 51

First derivatives of curves shown in Figure 50

recognize that $\frac{k}{2m + 2}$ makes it possible to compare all curves, since they have become independent of the size of "A" and "m." The weighted mean relative growth rate may be determined similarly to equation [30]. That is,

$$\frac{1}{A} \int_0^A \frac{k}{1-m} \left(\frac{A}{G}\right)^{1-m} - 1 \, dG = \frac{k}{m} \quad [31]$$

$G = A$
 $G = 0$

The value, T, is the reciprocal of $\frac{k}{2m + 2}$, and indicates the time required for major part - 90 to 95% - of the growth to take place; L_T , the length of the leaf in mms at time T; and $L_{T/A}$, proportion of the total growth expressed in per cent that has taken place by time T.

Table 33 recapitulates the definition of the aforementioned constants.

The elongation of alternate leaves up the stem of the control plants was evaluated by Richards' procedure and the data is presented in Table 34. There was a tremendous range in the total length, A, of the leaves at different positions up the stem. Constants directly related to A such as I, L_T , and $\frac{A k}{2m + 2}$ had comparable ranges in their values. Since the values for I/A, varied little for different leaves on the two plants, the values for "m" were fairly constant. Also, the values for k, the rate constant for the growth function, varied little over the great variation in total growth of leaves. Further, the weighted mean relative growth rate, k/m , varied but little for leaves showing great differences in total growth.

Table 33

Definition of Richards' Constants

b	:	the intercept of the growth function with the ordinate for zero time.
A	:	the asymptote of leaf length.
m	:	an empirical factor to adjust skewed distribution towards normality.
k	:	the rate factor of the growth function.
I	:	the inflection point of the sigmoid curve.
$m \frac{1}{1-m}$:	I/A , providing for the quantification of "m."
$\frac{k}{2m + 2}$:	the <u>proportional</u> average rate of leaf elongation of the whole length.
$\frac{Ak}{2m + 2}$:	the weighted mean elongation rate per day.
T	:	$\frac{1}{k/2m + 2}$, or the time required for the major part of the leaf growth to take place.
k/m	:	the weighted mean relative growth rate; i.e., the actual relative growth rate at point of inflection.
L_T	:	the length of the leaf at time T.
L_T/A	:	the proportion of the total elongation that has taken place in time T.

Growth constants for selected leaves on control plants

Constant	Plant 6					
	Leaf No.					
	1	3	5	7	9	11
A, in mms	221	304	383	462	440	410
I, in mms	96	134	166	201	184	186
I/A , or $m \frac{1}{1-m}$.434	.441	.434	.434	.418	.454
m	1.42	1.48	1.42	1.42	1.31	1.58
b	2.550	2.026	2.172	2.400	2.069	5.836
k	.256	.267	.246	.236	.266	.296
$k/2m + 2$.053	.054	.051	.049	.058	.058
$A \cdot k/2m + 2$, in mms	11.8	16.5	19.6	22.7	25.7	23.7
k/m	.183	.183	.176	.169	.208	.189
T , or $\frac{1}{k/2m + 2}$, in days	18.9	18.5	19.6	20.4	17.2	17.2
L_T , in mms	210	292	366	442	407	385
L_T/A , in %	95.0	96.0	95.6	95.7	92.5	93.9

Constant	Plant 12					
	Leaf No.					
	1	3	5	7	9	11
A, in mms	209	302	390	444	410	368
I, in mms	92	135	165	192	190	160
I/A , or $m \frac{1}{1-m}$.440	.447	.423	.432	.463	.435
m	1.47	1.52	1.34	1.41	1.65	1.43
b	2.363	3.320	5.150	2.801	8.585	3.490
k	.262	.285	.252	.252	.318	.275
$k/2m + 2$.053	.057	.054	.052	.060	.057
$A \cdot k/2m + 2$, in mms	11.1	17.1	21.0	23.1	24.6	20.8
k/m	.178	.187	.188	.179	.193	.192
T , or $\frac{1}{k/2m + 2}$, in days	18.9	17.5	18.5	19.2	16.7	17.5
L_T , in mms	200	289	371	423	390	349
L_T/A , in %	95.7	95.7	95.1	95.3	95.1	94.8

The significance of the variation in growth is shown in Table 35. Even though inherent physiological predetermination induced great differences in total growth of leaves at different positions on the stem, these leaves showed remarkable constancy in relative growth rate as indicated by the data in Tables 34 and 35. In other words, genetic factors were determining the lengths of the leaves of the control plants with environmental effects incurring but little modification. The foregoing is important information in this study seeking to quantify the effects of imposed environmental stresses on leaf growth.

To gain some insight as to the extent to which imposed treatments affected the magnitude of Richards' growth functions, the growth of the fifth leaf on all plants was analyzed. Table 36 presents the findings. A glance at the data indicates that treatment had a marked effect on the magnitude of all factors. These effects may be better evaluated by reference to the following summary tables.

Table 37 shows that water regimes had a very pronounced effect on the ultimate length of the fifth leaves, and that salt levels had an even greater effect. The effects of water regime and salt levels were sufficiently straightforward that there was no interaction in their effects. These findings are consistent with most of those from the vast literature on the effects of salinity and water regime on plant growth.

Table 35

Mean values of growth functions with indication of significance (control plants only)

Constant	Mean value for leaf No.										F ₁ /	D ₂ /
	1	3	5	7	9	11	11	11	11	11		
A, mms	215	303	386	453	425	389	389	389	389	389	96***	54
I, mms	94	134	165	196	187	173	173	173	173	173	43***	35
I/A	.437	.444	.428	.433	.440	.440	.444	.444	.444	.444	.32	.067
m	1.44	1.50	1.38	1.41	1.48	1.50	1.50	1.50	1.50	1.50	.35	.506
k	.259	.276	.249	.244	.292	.285	.285	.285	.285	.285	2.79	.071
$\frac{k}{2m+2}$.0530	.0555	.0525	.0505	.0590	.0575	.0575	.0575	.0575	.0575	13.7**	.0052
$\frac{Ak}{2m+2}$, mms	11.4	16.8	20.3	22.9	25.1	22.2	22.2	22.2	22.2	22.2	42***	4.6
k/m	.180	.185	.182	.174	.200	.190	.190	.190	.190	.190	3.3	.030
T, days	18.9	18.0	19.0	19.8	16.9	17.3	17.3	17.3	17.3	17.3	12.3**	1.87
L _T , mms	205	290	368	432	398	367	367	367	367	367	135***	43
L _T /A, %	95.3	95.8	95.3	95.5	93.8	94.3	94.3	94.3	94.3	94.3	1.74	3.56

1/ Variance ratio: *** probability exceeds 0.001

** probability exceeds 0.01

* probability exceeds 0.05

2/ Difference between any two means required for 0.05 significance.

Table 36

Growth constants for the 5th leaves of plants under various treatments

Growth function	"Wet" treatments					
	OS-W		MS-W		HS-W	
	#6	#12	#3	#11	#4	#7
A, in mms	383	390	250	291	216	214
I, in mms	166	165	85	100	82	80
I/A	.434	.423	.340	.344	.379	.374
m	1.42	1.34	0.85	0.87	1.06	1.03
b	2.172	5.150	1.594	1.489	1.198	1.087
k	.247	.252	.211	.207	.174	.179
k/2m + 2	.051	.054	.057	.055	.042	.044
Ak/2m + 2, mms	19.5	21.1	14.3	16.0	9.07	9.42
k/m	.174	.188	.248	.238	.164	.174
T, days	19.6	18.5	17.5	18.2	23.8	22.7
L _T , mms	366	371	236	270	204	203
L _T /A, %	95.6	95.1	94.4	92.8	94.4	94.9

Growth function	"Dry" treatments					
	OS-D		MS-D		HS-D	
	#5	#9	#1	#10	#2	#8
A, in mms	340	333	233	241	160	160
I, in mms	124	125	79	80	45	43
I/A	.365	.375	.339	.332	.281	.269
m	.98	1.04	.85	.82	.61	.57
b	1.198	1.087	1.310	1.570	1.782	2.125
k	.173	.199	.108	.135	.107	.135
k/2m + 2	.044	.049	.029	.037	.033	.043
Ak/2m + 2, mms	15.0	16.3	6.76	8.92	5.28	6.88
k/m	.176	.191	.127	.165	.175	.237
T, days	22.7	20.4	34.5	27.0	30.3	23.3
L _T , mms	318	310	213	224	156	151
L _T /A, %	93.5	93.1	91.4	92.9	97.5	94.4

Table 37
 Analysis of variance of A values

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	mms
Wet	386	270	215	291
Dry	336	237	160	244
Mean	361	254	187	

Source of Variance	F ^{1/}
Water regimes	41.5***
Salt levels	200.5***
Water X salt	.82

^{1/}Variance ratio: *** Probability exceeds 0.001
 ** Probability exceeds 0.01
 * Probability exceeds 0.05

The data for the leaf growth at the inflection points are shown in Table 38. The findings are analogous to those for the asymptotes excepting that there was a significant difference between the quantitative response to salinity in the "dry" cultures as compared to the "wet" cultures. The situation is reflected by the mean values found for other growth functions.

The summary of the findings for the function, $I/A = m^{\frac{1}{A}}m$, is given in Table 39. Treatment effects accounted for 99.3% of the variance for values recorded for I/A with response to salt being quite different in the "wet" cultures than in the "dry" cultures. One should particularly note the seemingly high value for I/A in the HS-W treatment.

Since the value of Richards' "m" is derived from I/A , it is to be expected that the analysis of variance for "m" values would show similar findings, Table 40, as those for I/A . It is particularly important to note that the imposed treatments had a tremendous impact on the value of "m" as compared to the finding that "m" showed no significant variation among the leaves of the control plants even though they varied greatly in size. Thus, the data in Table 40 show that the degree of skewness of the rate curves for leaf growth varied markedly with treatment.

The analysis of the values for the rate of change in the growth function as modified by "m" is shown in Table 41. The effects of water regimes and salt levels accounted for 98.9 per cent of the variability observed for k, with no interaction in the impact of these two environmental factors.

Table 38

Analysis of variance of I values

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	mms
Water	165.5	92.5	80.9	113.0
Salt	124.5	79.5	44.0	82.7
Mean	145.0	86.0	62.5	

Source of Variance	F _{1/}
Water regimes	139***
Salt levels	364***
Water X salt	11.5**

1/Variance ratio: *** Probability exceeds 0.001
 ** Probability exceeds 0.01
 * Probability exceeds 0.05

Table 39
 Analysis of variance of values for I/A

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	mms
Wet	.428	.342	.376	.382
Dry	.370	.335	.275	.327
Mean	.399	.339	.326	

Source of Variance	$F^{1/}$
Water regimes	242***
Salt levels	161***
Water X salt	59***

$1/$ Variance ratio: *** Probability exceeds 0.001
 ** Probability exceeds 0.01
 * Probability exceeds 0.05

Table 40
 Analysis of variance for "m" values

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	mms
Wet	1.38	.86	1.04	1.10
Dry	1.01	.83	.59	.81
Mean	1.19	.85	.82	

Source of Variance	F _{1/}
Water regime	202***
Salt levels	148***
Water X salt	43.5***

1/Variance ratio: *** Probability exceeds 0.001
 ** Probability exceeds 0.01
 * Probability exceeds 0.05

Table 41
Analysis of variance of K values

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	mms
Wet	.249	.209	.176	.211
Dry	.186	.121	.121	.143
Mean	.218	.165	.149	

Source of Variance	F ^{1/}
Water regime	143***
Salt levels	52***
Water X salt	2.8

^{1/}Variance ratio: *** Probability exceeds 0.001
 ** Probability exceeds 0.01
 * Probability exceeds 0.05

In view of the findings in Tables 40 and 41, it is remarkable that there was found to be such little significance in Table 42 for the mean values of k/m , the weighted mean relative growth rate. This is explainable by reference to Table 36 where the replicate values for k/m are given for treatments MS-D and HS-D. Agreement was poor. The maximum in soil moisture stress in the "dry" series of cultures usually was attained on different days in replicate treatments. Thus, the fifth leaves on replicate plants were at different stages of growth when the maximum in soil moisture stress was imposed. This resulted in dissimilarity in the growth response curves between replicates; and the dissimilarity is reflected in the divergent values for k/m , especially in the MS-D and HS-D treatments. Thus, k/m is indicating the degree of specificity in the form of the growth curves.

The proportional growth rate per day, $\frac{k}{2m + 2}$, is similarly affected as explained in the preceding paragraph. However, Table 43 does indicate that water regimes had a highly significant effect on the latter growth function.

The weighted mean elongation rate per day, $\frac{Ak}{2m + 2}$, is greatly influenced by the magnitude of A. This is shown in Table 44 showing water regimes and salt levels having a tremendous impact on the size of this function with no interaction between treatment means. In fact, the change in value for $\frac{Ak}{2m + 2}$ with increasing environmental stresses was just about orthogonal as one would hope to find in textbooks presenting illustrative theory.

Table 42
 Analysis of variance for values of k/m

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	
Wet	.181	.243	.169	.198
Dry	.183	.146	.206	.178
Mean	.182	.194	.187	

Source of Variance	$F^{1/}$
Water regime	3.51
Salt levels	.50
Water X salt	15.4**

$^{1/}$ Variance ratio: *** Probability exceeds 0.001
 ** Probability exceeds 0.001
 * Probability exceeds 0.05

Table 43

Analysis of variance for values of $k/2m + 2$

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	mms
Wet	.052	.056	.043	.050
Dry	.046	.033	.038	.039
Mean	.049	.044	.040	

Source of Variance	$F_{1/}$
Water regime	22.4**
Salt levels	4.74
Water X salt	5.96*

$1/$ Variance ratio: *** Probability exceeds 0.001
 ** Probability exceeds 0.01
 * Probability exceeds 0.05

Table 44
 Analysis of variance for values of $\frac{Ak}{2m + 2}$

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	mms
Wet	20.3	15.15	9.24	14.90
Dry	15.6	7.84	6.08	9.86
Mean	18.0	11.50	7.66	

Source of Variance	F ^{1/}
Water regime	63.2***
Salt levels	90.0***
Water X salt	3.7

^{1/}Variance ratio: *** Probability exceeds 0.001
 ** Probability exceeds 0.01
 * Probability exceeds 0.05

Since the values for T (time required for major part of growth--see Table 45) are reciprocals of those for $\frac{k}{2m + 2}$, they reflect the divergence among replicates in the "dry" treatment mentioned for $\frac{k}{2m + 2}$ and k/m. Overall, the table indicates leaves under elevated environmental stresses take longer to attain their growth, but those under MS-W treatment tended to make their growth in less time than the control, whereas those under MS-D required the most time. Observations on leaves additional to the fifth, suggest that this response to a modicum of salinity under the two different water regimes may be significant.

The amount of growth taking place during time, T, on the fifth leaf of each plant is shown in Table 46. Salt levels and water regimes accounted for 98.5 per cent of the variance in values for L_T with no interaction in the effects of these two environmental factors.

Richards predicted that values for $L_{T/A}$, the proportion of the elongation taking place during time T would always be between 90 and 95%. The evidence in Tables 35 and 47 indicate that he was "right on the beam."

For the convenience of quick recapitulation, the variance ratios for the different treatment effects are given in Table 48.

A great volume of additional statistics could be presented on the growth of all the other leaves of all the plants in this study, but it is doubtful if the effort would produce very much additional information. Richards'

Table 45
Analysis of variance of T values

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	
Wet	19.0	17.8	23.2	20.0
Dry	21.5	30.7	26.8	26.4
Mean	20.3	24.3	25.0	

Source of Variance	F ^{1/}
Water regime	12.66**
Salt levels	2.74
Water X salt	3.47

^{1/}Variance ratio: *** Probability exceeds 0.001
 ** Probability exceeds 0.01
 * Probability exceeds 0.05

Table 46
 Analysis of variance of values for L_T

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	mms
Wet	368	253	203	275
Dry	314	218	153	229
Mean	341	236	178	

Source of Variance	$F_{1/}$
Water regime	55.5***
Salt levels	235.0***
Water X salt	.95

$1/$ Variance ratio: *** Probability exceeds 0.001
 ** Probability exceeds 0.01
 * Probability exceeds 0.05

Table 47
 Analysis of variance of values for $L_{T/A}$

Water regime	Salt levels			Mean
	OS	MS	HS	
	mms	mms	mms	
Wet	95.3	93.3	94.6	94.4
Dry	93.3	92.1	95.9	93.8
Mean				

	Source of Variance		F	
	Water regime		.06	
	Salt levels		.34	
	Water X salt		.15	

Table 48
 Variance ratios for treatment effects

	Variance ratios ^{1/}		
	Water regime	Salt levels	W X S
A	41.5 ***	200.5***	.82
I	139.0 ***	364.0***	11.5 **
I/A	242.0 ***	161.0***	59.0 ***
m	202.0 ***	148.0***	43.5 ***
k	143.0 ***	52.0***	2.8
k/2m + 2	22.4 **	4.74	5.96**
$\frac{Ak}{2m + 2}$	63.2 ***	90.0***	3.7
k/m	3.51	.50	15.4 **
T	12.66**	2.74	3.47
L _T	55.5 ***	235.0***	.95
L _{T/A}	.06	.34	.15

^{1/}*** Significant at 0.001 probability.

** Significant at 0.01 probability.

* Significant at 0.05 probability.

procedure does give a better insight into the quantitative characterization of plant growth. However, one is left with the suspicion that the procedure is much more productive of statistics than of botanical or ecological information.

Although the procedure is quite effective in correcting for asymmetry in sigmoid growth curves, it was not adequate for the main purpose of this investigation. This may be illustrated by reference to Figure 52. The derived regression line provides a very good fit of the observations for most purposes. However, the deviations do not occur at random: during the forepart of the growth period, all observations are above the regression line, and during the middle part they are all below. In a study relating day-to-day variations in growth with environmental effects, use of this regression line for the general trend of growth would introduce considerable bias. The obviously curvilinear trend of the observation in Figure 52 as well as those for other leaves must be recognized. Consequently, other procedures than use of the corrective factor "m" were followed.

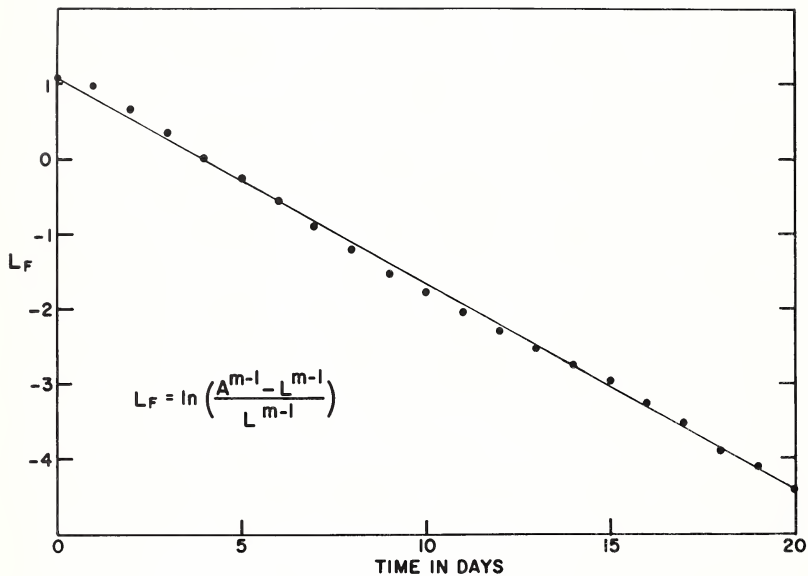


Figure 52

Data for the leaf growth function, L_F , involving modification effected by use of Richards' "m."

Areal Expansion of Leaves

As shown by Figure 53, conversion of the data for leaf elongation to leaf area (equation [18]) changed the general shape of the logistic curve for growth; rate of increase was relatively slower when leaves were small, and relatively more rapid during major expansion. Nevertheless, it will suffice to say that adapting equation [3] to derive constants for areal expansion for individual leaves was disappointing. The relation of actual values for ΔA for each leaf plotted in relation to values, $\Delta A'$, resulted in the same objections shown for the ΔL values in Figure 49.

It was deemed advisable to total the values for leaf area for all leaves on a given plant for each day. It was assumed that this step would iron out some of the apparent vagaries in data for individual leaves. The growth function $\ln\left(\frac{S-A}{A}\right)$, (from equation [6]), is plotted against time in Figure 54. The trend of the observations during the first 10 days of leaf growth was quite different than that during the remainder of the experimental period. This is shown by the two linear regression curves in Figure 54. The same situation prevailed for all the other experimental plants.

Applying equation [2] to the values for total leaf area, with deletion of the first ten observations provided the data in Table 49. The coefficients of determination, r^2 , showed that most all of the variance in values of $\ln\left(\frac{S-A}{A}\right)$ was related to concomitant variance in t . Even though the

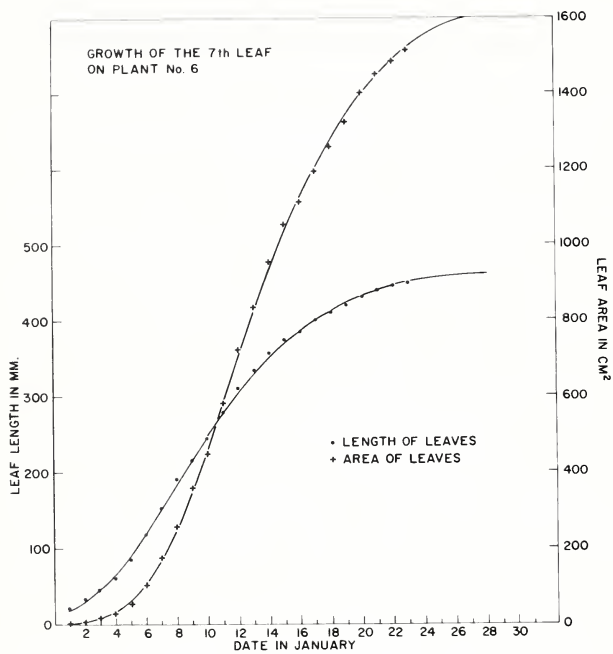


Figure 53

Change in conformation of a leaf growth curve on conversion
from linear measurement to area measurement

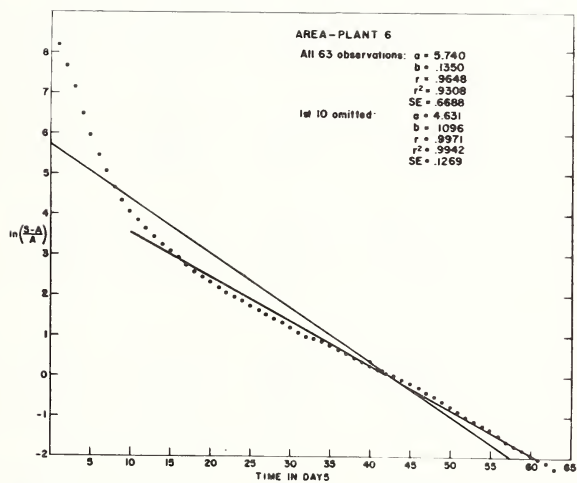


Figure 54

Relation of $\ln\left(\frac{S-A}{A}\right)$ to time on plant No. 6

Table 49

Statistics for linear relation between $\ln\left(\frac{S-A}{A}\right)$ and time
with first ten observations omitted

Treatment	Culture no.	$\ln a$	b	r^2	SE
OS-W	6	4.631	0.110	0.994	0.127
	12	4.692	0.112	0.991	0.163
MS-W	3	4.778	0.097	0.994	0.116
	11	4.681	0.098	0.993	0.133
HS-W	4	4.372	0.085	0.993	0.114
	7	4.687	0.096	0.993	0.126
OS-D	5	4.080	0.094	0.987	0.168
	9	4.263	0.099	0.985	0.186
MS-D	1	3.656	0.073	0.967	0.209
	10	3.517	0.075	0.975	0.182
HS-D	2	3.813	0.084	0.981	0.178
	8	3.941	0.095	0.981	0.202

standard errors of estimate appear to be small, these are indices of deviation in logarithmic values. On transformation, a similar effect to that shown in Figure 41 prevails; the variability in the predicted values for A are greater than might be indicated by the statistics in Table 49.

There appears to be relatively little variability for the values of $\ln a$ with treatment (Table 50). This statistic merely shows the intercept with the ordinate at zero time. Water regime had a marked effect on the value of this intercept, and the effect of salt differed within the two water regimes.

The statistic "b" is the growth rate index. There was good agreement between replicates and surprisingly little change in the value of "b" as affected by treatment. Yet, as shown by Table 51, treatments had a highly significant effect on the magnitude of the growth rate indices. The effects were of the general trend that might be expected, except that the value for "b" for the "MS-D" treatment seemed to be unduly low.

Although these statistics are of interest in showing the effect of imposed environmental stresses upon a growth index, the approach provides no means of evaluating effects of other environmental variables.

It may be mentioned that treating the growth function, $\ln\left(\frac{S-A}{A}\right)$, in relation to a cubic function of time as in equation [6] was just as disappointing as in the case of elongation of individual leaves.

Table 50

Mean Values for "ln a" as affected by treatment

Treatment means	OS	MS	HS	Ave.
Wet	4.662	4.729	4.530	4.640
Dry	4.172	3.586	3.877	3.878
Ave.	4.416	4.158	4.203	

Analysis of Variance

Effect	Degrees of freedom	Mean square	Variance ratio
Water	1	1.741171	115**
Salt	2	.076230	5.04
Water X Salt	2	.115567	7.63*
Error	6	.015129	

**Significant at 0.01

*Significant at 0.05

Table 51

Mean values for "b" as affected by treatment

Treatment means	OS	MS	HS	Ave.
Wet	0.111	0.098	0.092	0.100
Dry	0.097	0.074	0.089	0.087
Ave.	0.104	0.086	0.090	

Analysis of Variance

Effect	Degrees of freedom	Mean square	Variance ratio
Water	1	.000520	23.5**
Salt	2	.000349	15.8**
Water X Salt	2	.000125	5.67*
Error	6	.000022	

**Significant at 0.01

*Significant at 0.05

The plot of the actual values between $\ln(\frac{S-A}{A})$ and time in Figure 54 suggested that linearity might be approached by also including a logarithmic function of time. Thus, the daily values for total leaf area on each plant were used to derive respective constants in a modification of equation [6] as follows:

$$A = \frac{S}{1 + Kt^a e^{bt + ct^2 + dt^3}} \quad [32], \text{ or}$$

$$\ln\left(\frac{S-A}{A}\right) = \ln K + a \ln t + bt + ct^2 + dt^3 \quad [33].$$

In evaluating the leaf area data by equation [33], time was coded so that all values fell between one and 11. This avoided involvement of enormous numbers in deriving the coefficient for t^3 . Thus,

$$t = t_a \frac{10}{63} \quad [34]$$

where,

- t = value for time used in equation [33]
- t_a = the actual value of time in days from 1 through 63
- 10 = 11-1, the range of coded values
- 63 = total days involved.

The derived statistics are given in Table 52. Certain points stand out. The coefficients of determination, R^2 , were all exceedingly high. Most all of the variance in the growth function -- $\ln(\frac{S-A}{A})$ -- was associated with the logarithmic function of time. The computer found no variance in the growth function associated with the linear and quadratic

Table 52

Statistics derived for respective plants by use of Equation [33]

Treatment	Culture No.	Statistic	In K constant	ln t	t	t ²	t ³	R ² %	S.E.
OS-W	6	Regress.	8.1893	-3.949	-	-	-.00060		
		S.E.		.083			.0000	99.3	.225
		F		2277.			22.7		
OS-W	12	Regress.	8.8049	-4.388	-	-	-.00022		
		S.E.		.075			.0000	99.4	.204
		F		3408.			3.6		
MS-W	3	Regress.	7.5835	-3.255	-	-	-.00078		
		S.E.		.073			.0000	99.2	.202
		F		1980.			52.8		
MS-W	11	Regress.	8.0373	-3.663	-	-	-.00041		
		S.E.		.070			.0000	99.3	.193
		F		2740.			16.2		
HS-W	4	Regress.	7.0860	-3.019	-	-	-.00057		
		S.E.		.082			.0000	98.8	.227
		F		1351.			22.7		
HS-W	7	Regress.	7.3403	-3.135	-	-	-.00083		
		S.E.		.074			.0000	99.2	.201
		F		1804.					
OS-D	5	Regress.	8.2351	-4.108	-	-	.000	98.1	.347
		S.E.		.126					
		F		1070.					
OS-D	9	Regress.	8.1363	-4.110	-	-	.000	98.7	.285
		S.E.		.107					
		F		1485.					

Continued-----

Table 52 (continued)

Treat- ment	Culture No.	Statistic	ln K Constant	ln t	t	t ²	t ³	R ² %	S.E.
M MS-D	1	Regress.	6.8650	-3.193	-	-	-	98.5	.240
		S.E.		.087					
		F		1345.					
10	Regress.	7.0713	-3.449	-	-	-	97.5	.323	
	S.E.		.119						
	F		840.						

HS-D	2	Regress.	5.9785	-2.604	-	-	-.00091	98.4	.241
		S.E.		.089				-	
		F		859.			45.		
8	Regress.	6.2361	-2.840	-	-	-.00114	98.7	.240	
	S.E.		.088				-		
	F		1034.			72.			

functions of time, but the cubic function of time was significantly associated with growth variance in four of the treatments. One might conclude from Table 52 that equation [33] provided very excellent characterization of the data for accumulated foliar expansion.

The constants in Table 52 were used to calculate $\Delta A/\Delta t_a$ values -- increase in leaf area per day. These are plotted for plant No. 6 in Figure 55 as the smooth curve with the solid line. It has the typical shape of the derivative of a logistic curve. The actual observations for ΔA are plotted as dots with circled dots showing the means of each five successive observations. The dotted line shows the apparent trend line of the observed values. Obviously, the calculated values were quite inadequate for showing the trend of the observed differences. It is not unusual for the derivative of a mass curve to show a poor fit of the increments in data. Curves for other plants showed as poor or poorer relationships as that set forth for plant No. 6.

It is concluded that the derivation of constants for logistic growth curves is just an exercise in futility, if these curves are to be differentiated to attain the trend in daily growth increments for evaluation in relation to the daily status of environmental stresses.

The observed daily increments on total leaf area for each plant were evaluated by use of equations [7] and [8].

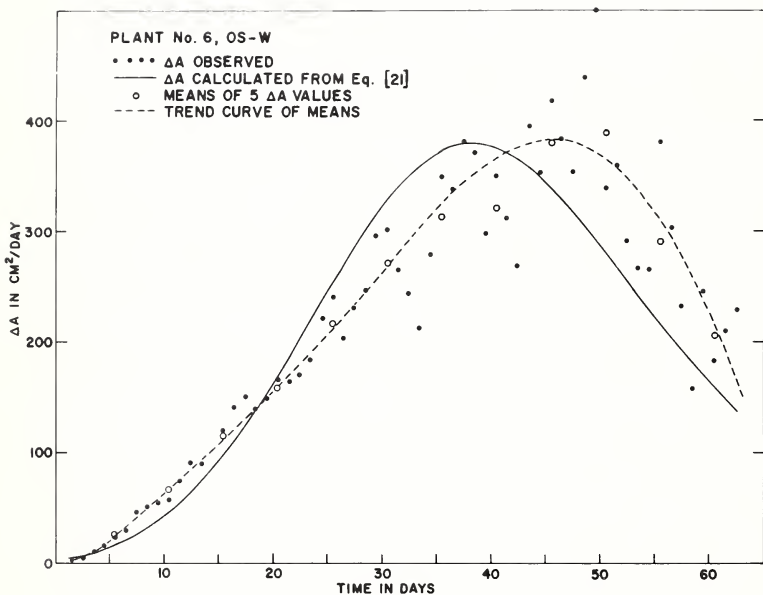


Figure 55

Relation between ΔA and time, showing the poor fit of the values derived by differentiating the mass curve

Time was transformed by use of equation [34]. The resulting regression coefficients and other statistics are shown in Table 53. On most of the plants, each function of time was associated with a significant reduction in variance for relative growth increments. Much less significance prevailed in the "dry" cultures than in the "set" series. This observation will be discussed forthwith.

In Figure 56, the solid curve shows the trend of the calculated values for ΔA of plant No. 6 by use of constants in Table 53 and in equation [7]. The actual values with means of successive 5's are also plotted. The locus of this curve agrees very well with the means of 5's. That is, use of equation [8] resulted in quite a different picture than that shown in Figure 55. In other words, one must conclude that the curve in Figure 56 is a good fit of the scatteration of the data.

Figure 57 is analogous to Figure 56, but presents the findings for plant No. 4 on the "HS-W" treatment. Daily growth increments are all relatively low and the scatteration is due to the effect of irrigation on diluting salinity. Thus, the standard error of estimate -- from Table 53 -- is about double for plant No. 4 as for plant No. 6. Nevertheless, the calculated trend line is a good average fit of the observed data.

Comparable observations for plant No. 5, on "OS-D" treatment, is shown in Figure 58. The tremendous scatter of the relative growth increments reflects the great influence

Table 53
 Statistics from equation [8] for each plant

Treatment	Plant No.	Statistic	ln K	ln t	t	t ²	t ³	R ² _%	S.E.
OS-W	6	Regress.	4.101	10.85	-5.06	.453	-.018	98.1	.152
		F		111.***	51.1**	41.0**	41.1**		
OS-W	12	Regress.	1.772	7.85	-2.54	.184	-.007	98.0	.170
		F		46.4**	10.3**	5.4*	5.6*		
MS-W	3	Regress.	3.412	7.53	-3.57	.331	-.013	96.9	.191
		F		35.8**	17.4**	15.3**	14.2**		
MS-W	11	Regress.	2.015	6.87	-2.47	.186	-.006	96.7	.203
		F		26.5**	7.4**	4.3*	3.3		
HS-W	4	Regress.	3.874	9.15	-4.78	.430	-.015	91.3	.291
		F		22.8**	13.5**	11.2**	9.4**		
HS-W	7	Regress.	2.840	8.18	-3.87	.343	-.012	91.2	.327
		F		13.5**	6.4*	5.1*	4.2*		
OS-D	5	Regress.	6.866	19.52	-10.28	.878	-.031	74.4	.614
		F		23.4**	14.1**	10.5**	8.6**		
OS-D	9	Regress.	3.670	12.07	-5.24	.384	-.012	66.4	.686
		F		6.35**	2.49	1.31	.84		
MS-D	1	Regress.	-.250	3.76	.453	-.246	.015	44.6	.836
		F		.45	.01	.43	1.1		
MS-D	10	Regress.	5.795	14.83	-7.72	.605	-.019	40.3	.831
		F		6.72*	3.85	2.36	1.44		
HS-D	2	Regress.	2.814	6.43	-3.11	.248	-.008	55.4	.534
		F		3.14	1.56	.99	.62		
HS-D	8	Regress.	4.699	12.50	-6.90	.615	-.023	47.7	.665
		F		7.68**	4.97*	2.96	3.42		

*Significant at 0.05

**Significant at 0.01

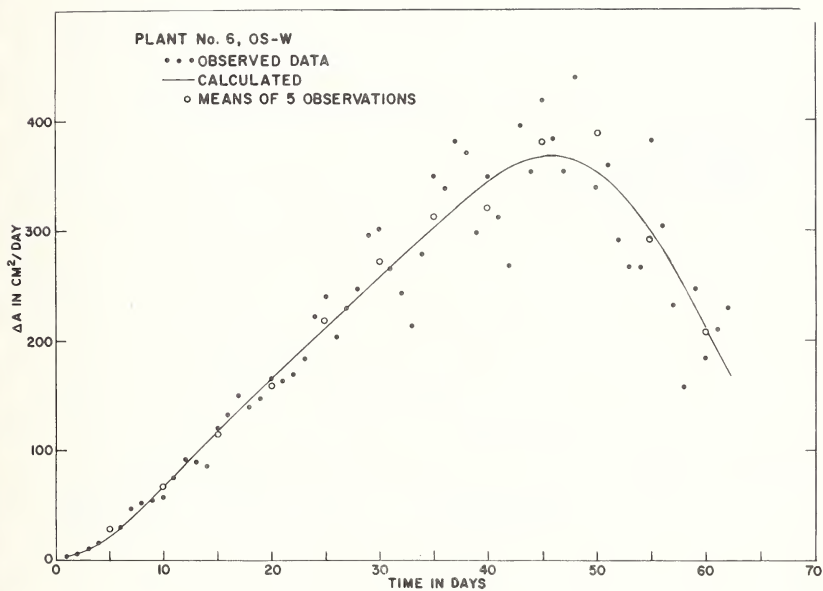


Figure 56
Relation between ΔA and time as derived by equation [8] for
a "0" salt-wet plant

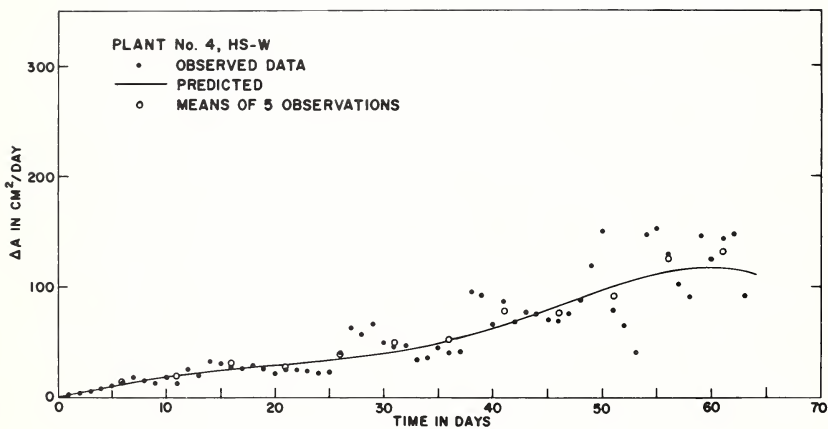


Figure 57

Relation between ΔA and time for a plant on the "high"
salt-wet treatment

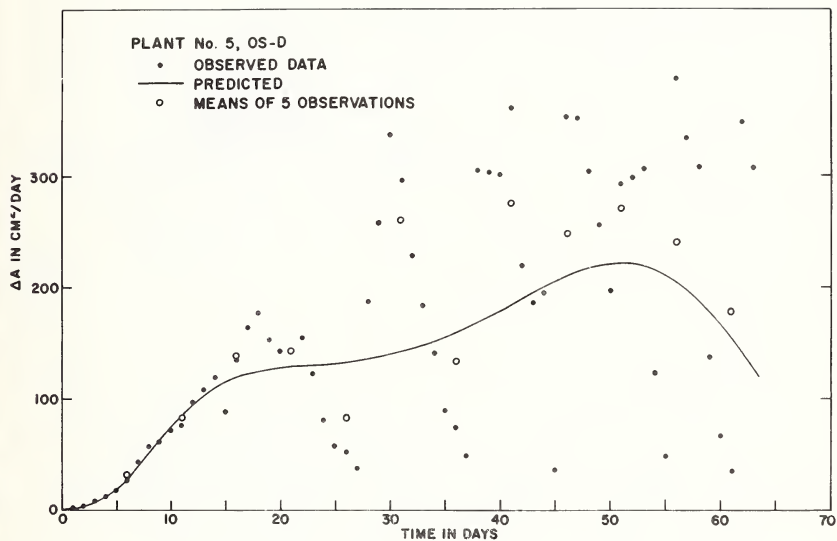


Figure 58

Relation between ΔA and time for a plant on the "0" salt-dry treatment

of the irrigation and drying cycles on daily foliar expansion. One may gain the suspicion that this curve is not necessarily the best fit of the observed data, but one hesitates to take issue with the dispassionate findings of a computer.

The calculated curve for plant No. 1 -- Figure 59 -- was found to be rather outre in relation to those for the other experimental plants. (This is also shown by the statistics in Table 53). It so happened that the experimental period terminated when this plant was making relatively good foliar expansion after a recent irrigation. The computer found this curve to be a good fit.

Growth Increment Ratio

The calculated values of ΔA for each plant for each day (referred to as " ΔA ") were used by dividing into the observed values for ΔA to give a growth increment ratio $\Delta A/\Delta A'$. On days a given plant made poorer growth than theoretical, the value of the increment ratio was less than one. It was greater than one on days of relatively good growth. The magnitudes of the growth increment ratio were related to environmental conditions by use of equation [9]. The derived statistics are presented in Table 54.

One must keep in mind certain strictures pertaining to the data in Table 54. Although variations in light and temperature were common to all plants, but those , osmotic pressure and matric suction were specific for a given culture.

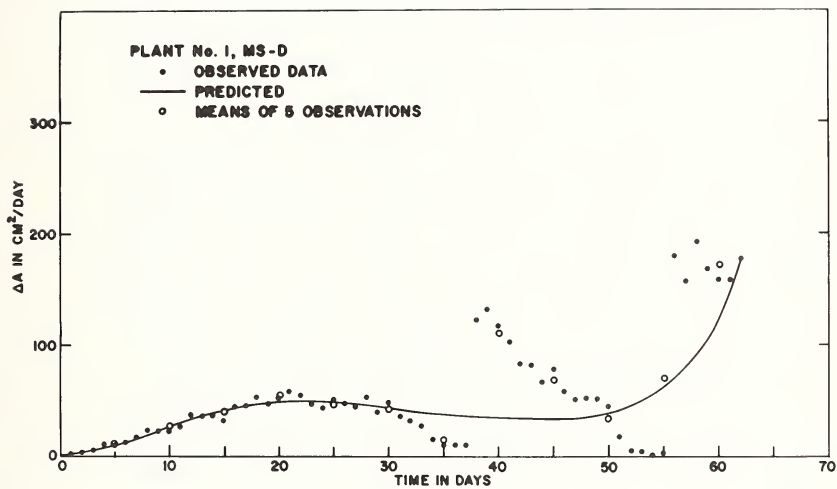


Figure 59

The relation between ΔA and time for a plant on the "med." salt-dry treatment

Thus, the variability for these factors in Table 54 refers only to the variability from the mean value for that specific culture. For example, salt level in the soil was one of the main variables in the experiment, yet the procedure under discussion does not take into account change in mean value of osmotic pressure between treatments; the regression coefficients in Table 54 only pertain to variability from the mean value for O.P. in a given treatment. Statistics for matric suction are similarly restricted.

The coefficients in Table 54 show that variations in the aerial environment appeared to have relatively little effect on growth increment ratio. Increased level of solar radiation did have a highly significant positive effect on the cultures without salt. One might anticipate that increasing light energy would have had a more definite positive effect on the salinized cultures, since one could presume that increased production of photosynthate would aid osmotic values of plant cells towards countering the increased diffusion pressure deficit in the soil solution.

Variations in temperature were without significant effect. Even though some of the regression coefficients associated with T were high, the respective standard errors of these coefficients were also very high. Any apparent concomitance between temperature and growth increment ratio was probably random. For example, the coefficient for the "MS-D" plants was highly positive and that for the "HS-D" plants highly negative.

Table 54

Coefficients for $\Delta A/\Delta A'$ versus environment

Treatment	Coefficient	ln K	Light	Temp.	Osmotic Press.	Matric suction	R ²	S.E.
OS-W	Regress.	-1.109	.144	.022	-.805	.176	20.7	.134
	S.E.		.042	.105	.336	.075		
	F		11.8**	.04	5.74*	5.52*		
MS-W	Regress.	-.104	.084	-.170	-1.967	.162	38.0	.155
	S.E.		.050	.121	.272	.068		
	F		2.83	1.97	52.4**	5.72*		
HS-W	Regress.	.908	.026	-.208	-2.244	.018	36.2	.252
	S.E.		.079	.193	.607	.201		
	F		.11	1.16	13.7**	.01		
OS-D	Regress.	.223	.544	.153	-1.240	-.515	74.1	.343
	S.E.		.109	.139	.213	.040		
	F		25.0**	1.21	22.2**	162.0**		
MS-D	Regress.	-.365	.444	1.324	-1.641	-1.219	63.1	.631
	S.E.		.211	.960	.548	.259		
	F		4.42*	1.90	8.97**	22.1**		
HS-D	Regress.	1.055	.251	-1.933	-2.142	-.167	50.6	.440
	S.E.		.137	1.188	.370	.414		
	F		3.33	2.65	33.4**	.16		

* Significant at 0.05

**Significant at 0.01

The statistics for the regressions on osmotic pressure were significant and highly consistent even though they pertained only to deviations from the mean value of O.P. within a culture. The magnitude of the regression coefficients increased considerably with increased level of salinity. One might have expected the effect of salt to have been more consistent. However, one must keep in mind that these regression coefficients show the linear relationship between logarithmic values. This is shown in Figure 60 in which the derived regressions between $\Delta A/\Delta A'$ and O.P. are shown for the three "dry" treatments -- specifically the loci between the circles on the regression lines. Light, temperature, and matric suction are held at constant values in using equation [9] for derivation of Figure 60. Humidity was of no effect and was eliminated by the computer. The curves are actually quite consistent when one takes into account that their loci occur at different levels of salinity. In fact, one could well have expected much larger regression coefficients for the "MS-D" and "HS-D" plants.

Values of $\Delta A/\Delta A'$ actually varied from 0.12 to 3.93 for the "MS-D" and from 0.11 to 3.84 for the "HS-D" plants. The regression lines in Figure 60 for these treatments were arbitrarily extended to these respective values as indicated by the crosses. Now, the daily values for osmotic pressure used in equation [9] were arbitrarily calculated as given under the section on "Basic Data." If one projects the terminal values (crosses) for $\Delta A/\Delta A'$ down to the abscissa

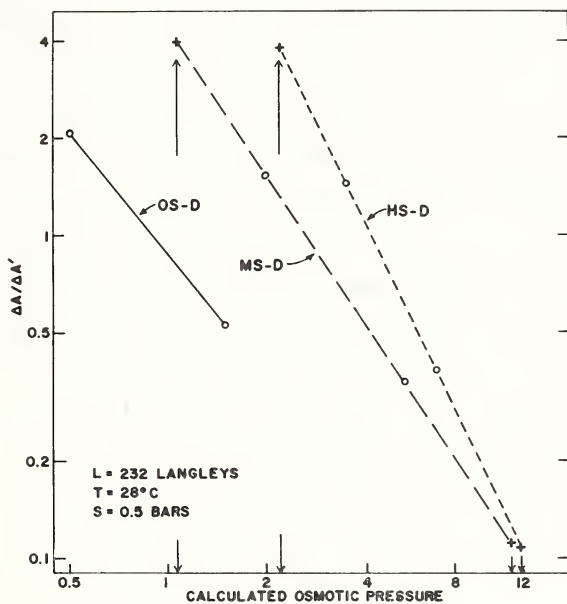


Figure 60

The ratio observed to calculated values of ΔA in relation to calculated osmotic pressure of the soil solution

for the salinized treatments, the "MS-D" curve implies that the effective salinity upon water availability shortly after an irrigation was only 1.1 atmos. osmotic pressure, and attained nearly 11 atmos. O.P. at the effective absorbing surfaces of the roots just before an irrigation. Similarly, projection to the abscissa from the crosses on the "HS-D" curve indicates a value of 2.2 atmos. O.P. shortly after an irrigation, and a value of 12 atmos just prior to irrigation.

Actually, one can make a strong case that the derived values for the range in osmotic pressure of given treatment by use of Figure 60 are much more valid than those calculated from average water and salt content of the total soil mass. The irrigation water supplied had an osmotic pressure of only about 0.13 atmos. One could even suspect that the maximum ΔA values observed following an irrigation were reflecting this nearly pure water and that the projected values for lower limit of O.P. in Figure 60 are far too conservative.

The foregoing discussion is important in that it emphasizes the lack of physical methods to fully characterize the effective osmotic pressure in a rhizosphere varying greatly in salt distribution and water content. The discussion implies that plant performance may better characterize the effective water potential in a heterogeneous system such as prevailed in the soil cultures of this experiment than the physical approaches that appear to be available.

The data for the "OS-D" treatment in Table 54 indicated that light, osmotic pressure, and matric suction had highly significant effects on the magnitude of the increment ratio, $\Delta A/\Delta A'$. Derived values for this ratio were determined for the "OS-D" plants by use of the logarithmic form of equation [9]. Temperature was locked in at the mean value of 28°C. Light and osmotic pressure were used at two selected levels, and $\ln \Delta A/\Delta A'$ was derived for a range of values of matric suction. The resulting matrix of relationships is shown in Figure 61.

At first glance, this figure looks pretty. Increasing level of solar radiation was associated with a marked increase in the growth increment ratio. Increasing osmotic pressure of the soil solution had the opposite effect. These responses were logical. Also, one could expect decreasing growth response with increasing matric suction, but these curves bear examining more closely. Consider the one at 300 langleys and 1.4 atmos. O.P. The ratio, $\Delta A/\Delta A'$, shows a value of 3 at 0.1 bars matric suction, and a value of 1 at 0.9 bars. Actually, there should have been little if any change in growth response over this range in matric suction. In fact, the regression coefficients for M.S. in the "wet" cultures in Table 54 were positive. These wet cultures were held at 0.1 - 0.5 bars. This same curve in Figure 61 shows that increasing 0.9 to 5.0 bars was associated with a decrease in $\Delta A/\Delta A'$ of from 1.0 to 0.4. This linear relationship to matric suction is indeed very questionable.

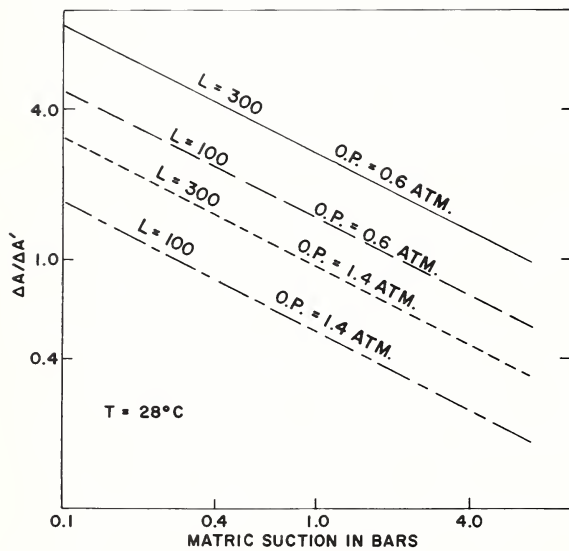


Figure 61

Relation of growth increment ratio to matric suction

Accordingly, the logarithmic form of equation [9] was modified as follows:

$$\ln \frac{\Delta A}{\Delta A'} = \ln K + a \ln L + b \ln T + c \ln P + d(\ln P)^2 + e \ln S + f(\ln S)^2 \quad [35]$$

There is little justification for relating all the details of the modifications of the regression coefficients from Table 54. It will suffice to mention that those for light and temperature remained unchanged. Computer logic threw out coefficients for the quadratic effect of P; i.e., $(\ln P)$, as well as those for the linear effect of S. In the "OS-D" treatment, $(\ln S)^2$ was found to have a value of -0.258 which was associated with an F value of -162. Figure 61 was replotted using the coefficient for $(\ln S)^2$ just given. The result is shown in Figure 62. These curves go through a maximum between 0.3 and 0.4 bars with increasing negative slope at the higher levels of matric suction. The trends imply that at soil moisture contents below field capacity, oxygen supply to the roots may limit plant response and at values of M.S. above one, the plant responded to decreasing availability of the water.

One can be impressed that a computer may not give out logical results if the input carries illogical constraints.

The statistics presented in Table 54 were disappointing in that the coefficients of determination R^2 , were rather low. For example, in the "OS-W" treatment, only 20 percent of the variance in $\ln \frac{\Delta A}{\Delta A'}$ was associated with logarithmic values

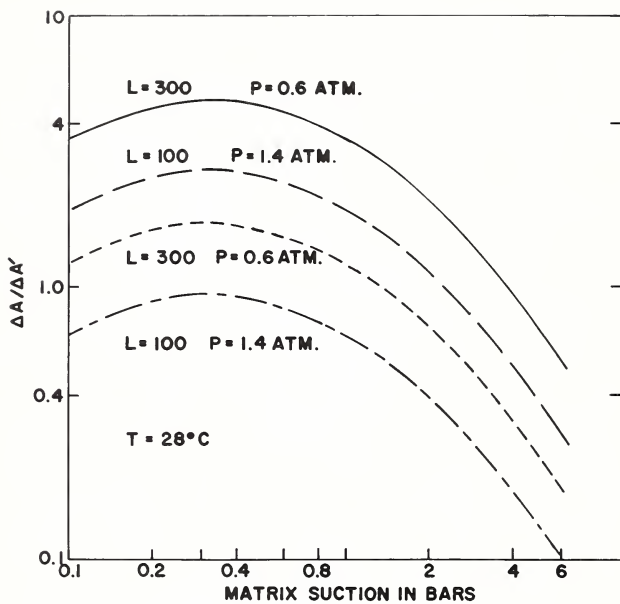


Figure 62

Figure 61 converted to curvilinear trends.

of prevailing environmental factors. It is of interest to explore why this was obtained. If a given environmental factor was having a definite effect, then all plants having the same treatment should respond similarly.

The paired observations for increment ratios of plants No. 6 and No. 12 on a given day are plotted in Figure 63. If two plants had responded identically to environmental conditions on each specific day, then all points would have fallen on the 45° line. The scatteration is quite pronounced. It was particularly disconcerting that there were so many points in quadrants II and IV. Those points arose from days on which the growth response of plant No. 6 was zagging while that of plant No. 12 was zigging. A teleologist might even conclude that there is something within the germ plasm of plants that appears to shun mathematical precision.

This lack of conformity in response of replicate plants readily explains the low value for R^2 in the "OS-W" treatment. It is of interest that plants in other treatments that incurred effective stresses in osmotic pressure or matric suction gave much higher values for the coefficient of determination.

One must conclude that evaluating the effects of environmental stresses on foliar expansion by use of the increment ratio was not satisfactory. Differences between treatments imposed the main changes in environmental stress and these were not taken into account; and they could not be taken

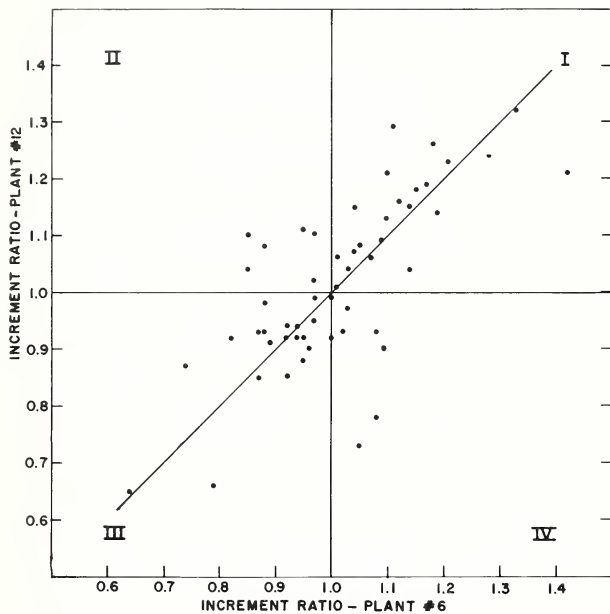


Figure 63

Comparison of increment ratios found for plant No. 6 in relation to plant No. 12, on given days

into account without resorting to highly involved mathematical gymnastics that reflected the regression coefficients for treatment trends. A different approach was deemed mandatory.

Fisher's Relative Growth Function. Fisher's (6) recommendation that growth, G, be evaluated in terms of the function $\frac{1}{G} \frac{dG}{dt}$ has not been used nearly as much as it should have been. Mathematically, this is identical with $d \ln G / dt$. It was adopted for use in this study as discussed under development of equations [10], [11], and [12]. It should be again stressed that it was essential to use the trend in total leaf area on the control plants as the biological measure of time rather than using actual time. Using the latter resulted in an erratic matrix of response trends under different treatments, whereas the biological measure avoided this difficulty. There was erratic dispersion of the values for $\frac{1}{A} \frac{dA}{dt}$ during the first week of observations. Hence, the first 10 days of records on each plant were omitted from this evaluation.

For the "OS-W" plants that were supposedly without experimentally imposed stresses, the logarithmic form of equation [11] provided the following constants:

$$\ln Q = 2.6815 - .4039 \ln\left(\frac{A}{1000}\right) - .006829 \left(\frac{A}{1000}\right)^2 \quad [36]$$

As shown in Figure 64, where $Q = \frac{1}{A} \frac{dA}{dt}$, this function expressed the relationship very closely. For example, the mean square variance associated with regression was found to be 39.063, and that of the residual variance to be 0.029, giving a variance ratio of 1342. The coefficient of determination indicated that 96% of the variance in $\ln Q$ was associated with concomitant variance in the function for leaf area.

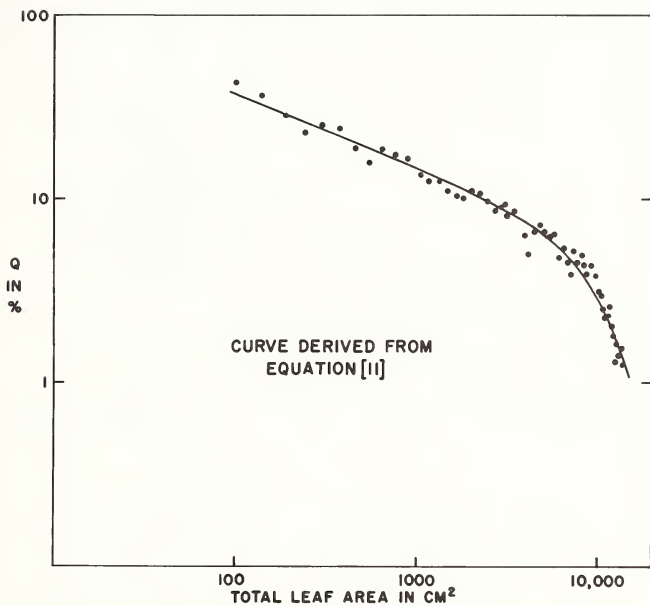


Figure 64

Relative growth in areal expansion of leaves as a function of total leaf area attained by the "control" plants

As pointed out in the discussion of equation [12], the constants derived in equation [36] were locked into the application of equation [12] for the data in each of the experimental treatments. This mathematical manipulation enabled the observed values of $\ln Q$ in each of the five treatments other than the control to be treated as deviations from control. Thus, all data from all treatments could be pooled for better evaluation of the net effect of specific environmental stresses.

Figure 65 presents the matrix of trends found for the six treatments with increasing soil moisture stress invariably depressing the locus of the respective curve. In each of the treatments, other than the control, there was marked dispersion of the day-to-day observations from the general trend.

Table 55 presents the constants attained for each treatment by use of equation [12] as modified by equation [36]. The term "now light" indicates the relationship to light occurring on the day the growth increment took place; and "old light" the relationship to light occurring on the day previous the specified growth increment.

In contrast to the data in Table 13 showing the definite effect of aerial environment upon evapotranspiration, the evidence in Table 55 indicates the aerial surroundings had relatively little impact on the day-to-day growth of the leaves. Maximum and minimum humidity were completely without effect. Maximum daily temperature tended to have a positive influence (non-significant) on daily growth in the "wet" cultures; a

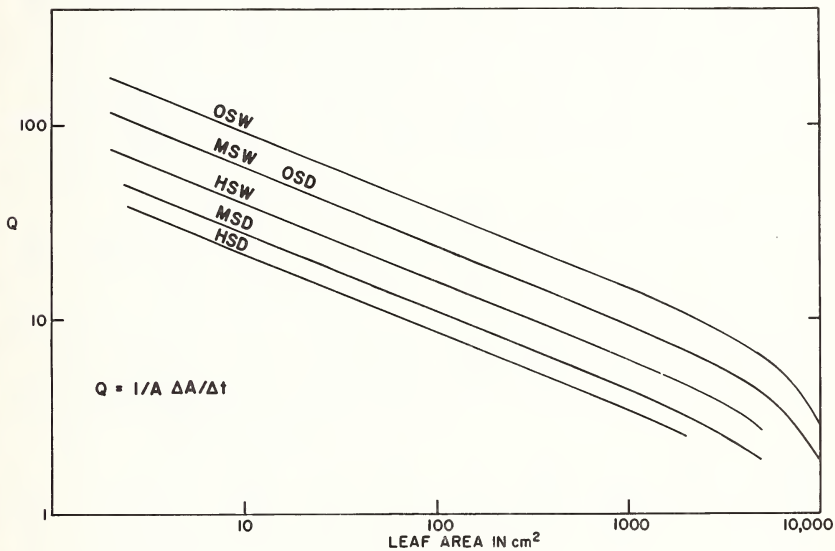


Figure 65

Matrix of trends for the six treatments calculated according to procedure used for Figure 64

Table 55

Coefficients for the relations between $\ln Q$ and environmental effects

Treatment	Coefficient	$\ln K^{1/}$ Adjust.	Now Light	Old Light	Temp.	Rel. Max.	Hum. Min.	O.P.	M.S.	R^2 %	S.E.
	Regress.	0.0	.146	.010	.275	-.016	.073	-.034	.040		
OS-W	S.E.		.058	.045	.145	.094	.084	.032	.060	20.2	.155
	F		6.30*	.05	3.57	.03	.75	1.11	.44		
	Regress.	-.4249	.035	.023	.401	.088	.116	-2.196	.732		
MS-W	S.E.		.086	.068	.210	.138	.124	.414	.069	78.1	.228
	F		.16	.11	3.63	.41	.87	28.1**	113.1**		
	Regress.	-.8506	.006	.179	.119	.015	.174	-2.249	-.086		
HS-W	S.E.		.088	.068	.219	.143	.128	.133	.057	93.7	.236
	F		.01	6.96**	.30	.01	1.86	286.0**	2.28		
	Regress.	-.4414	.329	.057	.038	.288	.046	.307	-.597		
OS-D	S.E.		.114	.094	.299	.195	.170	.028	.029	86.1	.321
	F		8.34**	.38	.02	2.20	.07	118.0**	409.0**		
	Regress.	-1.2094	.020	-.003	-1.464	.047	-.384	-6.733	.774		
MS-D	S.E.		.294	.217	.767	.455	.412	.475	.153	80.7	.749
	F		0.0	0.0	3.64	.01	.87	201.0**	25.6**		
	Regress.	-1.4512	-.143	.076	-1.653	-.304	-.105	-2.690	-.222		
HS-D	S.E.		.127	.100	.365	.24	.189	.071	.054	95.5	.350
	F		1.27	.59	20.6**	2.02	.31	143.4.0**	16.9**		

^{1/}This shows the magnitude of displacement from the "control" curve in Figure 65.

*Significant at 0.05 probability.

**Significant at 0.01 probability.

negative effect in the "dry" cultures. In most treatments the standard error of regression was sufficiently large to preclude significance, but there seems to be little question about the effect in the "HS-D" treatment. The "MS-D" plants provided a coefficient of similar magnitude. One might conclude that under drought, elevated temperature accentuates the effect of the drought, it accentuates internal water deficit. Under ample water supply, the higher temperatures tended to be associated with improved daily growth.

Daily solar radiation had little effect upon the growth of the plants with the exception of the positive effect noted for the unsalinized plants. One should look upon the significant effect of "old" light on the "HS-W" plants with suspicion. The outcome was quite anomalous with the non-effects of "old" light on all other plants.

Salinization of the soil had an exceedingly marked effect in depressing daily growth. One would expect the regression coefficients for the effects of added salt to be all of the same magnitude. Three of the four salted soils provided coefficients of -2.2 to -2.7 and the "MS-D" cultures gave rise to a much larger value of -6.7. It must be noted that matric suction was indicated as having a markedly positive effect on daily growth in the "MS-D" treatment. This effect was most likely not an actuality. Rather, as will be shown later, there was intercorrelation between values for osmotic pressure and those for matric suction (both increase with decreasing water content of soil). Thus, the positive value for regression with

matric suction in the "MS-D" treatment in the computer print-out was undoubtedly compensatory for the unduly high regression with osmotic pressure.

A comparable situation to the foregoing previlas in the data for the "OS-D" treatment. The soil was unsalinized and elevated matric suction was the dominant environmental factor. The marked negative effect of matric suction is evident, but change in osmotic pressure due to nutrient solutes was indicated as having a highly positive effect on growth. This latter observation is unquestionably not an actuality, but merely another mathematical extrusion from the intercorrelation between osmotic pressure and matric suction.

It is also of interest that a highly positive regression prevailed between matric suction and daily growth in the "MS-W" cultures even though matric suction varied only between 0.1 and 0.3 bars. This is part of the evidence that the ecology of the rhizosphere was impaired at the lower limit of soil moisture tension imposed.

It appeared possible that a clearer picture of the environmental effects would emerge if the data were discrete treatments pooled. As shown in Table 56, data from the "wet" cultures were pooled; that from the dry pooled; and then all data pooled. The evidence in this table provides quite a different impression than that in Table 55. Both "now" and "old" light were shown to have a highly significant positive effect on daily growth in the "dry" treatments and for all cultures pooled. It is especially surprising that temperature was found to have a significant

Table 56

Coefficients for the relations between $\ln Q$ and environmental effects
with data from "wet" and "dry" cultures pooled

Treatment	Coefficient	$\ln K$ Adjust.	Now Light	Old Light	Temp.	Rel. Max.	Hum. Min.	O.P.	M.S.	R^2 %	S.E.
"Wet" pooled	Regress	-.4252	.028	.064	.382	.067	.129	-.359	.561		
	S.E.		.067	.051	.165	.109	.097	.021	.024	73.6	.310
	F		.17	1.53	5.35*	.38	1.77	292.0**			
"Dry" pooled	Regress	-1.0339	1.094	.596	2.092	.709	1.723	-.474	-.433		
	S.E.		.234	.189	.634	.409	.342	.079	.071	32.4	1.173
	F		21.8**	9.91**	10.9**	3.00	25.3**	36.2**	37.6**		
All pooled	Regress	-.7296	.826	.502	1.975	.583	1.342	-.365	.077		
	S.E.		.139	.110	.358	.236	.202	.045	.043	22.5	.960
	F		35.5**	20.8**	30.5**	6.08**	44.1**	64.8**	3.19		

*F value at 0.05 probability = 3.85

**F value at 0.01 probability = 6.75

positive effect in all pooled groups, in contrast to the marked negative effect found for the MS-D and HS-D treatment. Even the humidity inputs were found to have a significant impact in the pooled data for daily growth. The effects of increasing osmotic pressure in the substrata were quite consistent in all pooled groups; but those of matric suction were highly positive (non-significant) in the "wet" cultures; highly negative in the "dry" cultures; and of no impact when all data were pooled.

There is no justification of further discussion of the above finding other than that they should be regarded with deep suspicion. The relatively low value of 0.474 for R ($R^2 = 0.225$) found for the "all pooled" relationships reveals that this was an exceptionally poor accounting for the variance in $\ln Q$. Another approach was mandatory.

There is no valid reason to assume that the relation between $\ln Q$ and various environmental inputs should be linear. For example, one may readily rationalize from the evidence available in the literature that growth of these plants should have approached a maximum at values of matric suction in the range of 0.3 to 1.0 bars. One could expect less growth at 0.1 bars due to oxygen deficiency in the rather wet soil; and a decrease in leaf growth as matric suction increased beyond one bar (4). It would be rational to assume little or no change in growth response at values for osmotic pressure ranging from 0.5 to 1.5 atmospheres with decreased daily growth at higher levels of osmotic pressure.

In line with the foregoing, equation [12] was modified so that the logarithmic form was as follows:

$$\ln Q = \ln K + a \ln \frac{1}{A} + b A^2 + f \ln L + g \ln T + h \ln P + i (\ln P)^2 + j \ln S + k (\ln S)^2 \quad [37]$$

That is, the relations of $\ln Q$ to $\ln P$ and $\ln S$ were treated as simple parabolic functions with humidity eliminated as an environmental input. The results are shown in Table 57. In stark contrast to the findings in Table 56, equation [37] produced results showing no effect of the aerial environment on daily plant growth; whereas, the magnitude of the variance ratios indicated that variations in $\ln P$ and $\ln S$ were having a tremendous impact on $\ln Q$. The regression coefficients for both the first and second degree effect of $\ln P$ were fairly consistent for all categories of pooling. They were consistently negative and similar in magnitude. All coefficients for both the first and second degree effect of $\ln S$ had highly significant variance ratios.

However, it is pertinent to note that the regression coefficients were markedly positive for the "wet" cultures (range 0.1 to 0.4 bars); and were definitely negative for the "dry" cultures and for the total pooling of data. It is of special interest to note that the values for the coefficient of determination, R^2 , were much higher in Table 57 than in Table 56. Use of equation [37] was far more effective in accounting for the variance in $\ln Q$ than equation [12].

There is no question that variations in osmotic pressure and matric suction were key environmental inputs affecting plant response. When these inputs were not adequately characterized

Table 57

Relationships of $\ln Q$ to environmental factors with $\ln P$ and
 $\ln S$ treated as parabolic functions

Treat- ment	Coeffi- cient	$\ln K$ Adjust.	$\ln L$	$\ln T$	$\ln P$	$(\ln P)^2$	$\ln S$	$(\ln S)^2$	R^2 %	S.E.
	Regress.	-.4252	.031	.075	-.805	-.332	1.267	.757		
"Wet" pooled	S.E.		.040	.097	.044	.056	.068	.060	86.8	.220
	F		.63	.59	336.0**	86.0**	342.0**	158.0**		
	Regress.	-1.0339	.198	.165	-1.432	-.871	-.202	-.427		
"Dry" pooled	S.E.		.116	.303	.059	.046	.042	.026	79.9	.639
	F		2.90	.29	596.0**	352.0**	23.0**	264.0**		
	Regress.	-.7296	.086	.283	-1.354	-.840	-.169	-.430		
All Pooled	S.E.		.066	.164	.041	.032	.023	.017	77.6	.515
	F		1.73	2.99	1076.0**	669.0**	53.4**	643.0**		

**F value at 0.01 probability = 6.75

as in equation [12], the computer assigned variance in $\ln Q$ to wherever it might fit with the results shown in Table 56.

Using the coefficients for the fully pooled data in Table 57, Figure 66 shows the relation of Q to P on logarithmic scales at two values of total leaf area, and with matric suction held at 0.2 and 4.0 bars, respectively. Solar radiation and maximum temperature were held at their means. These curves all show a maximum in daily growth at 1.2 atmos osmotic pressure, with a depressing effect at both higher or lower levels of osmotic pressure. One must keep in mind that these curves have the constraint that they must be parabolas whether or not the true relationship between $\ln Q$ and $\ln S$ is actually parabolic. One could well rationalize that these curves should not have had a downward trend at values of osmotic pressure below 1.2 atmos. The loci of the curves above 1.2 atmos. osmotic pressure appear plausible.

The curves in Figure 67 should also be considered along with those in Figure 66. The relation between $\ln Q$ and $\ln S$ is shown in Figure 67 by use of the coefficients for the fully pooled data in Table 57. In these curves, the maximums in daily growth response was found to be at 0.3 bars--the value that is usually quite close to the field capacity of a soil. Deduction on the basis of a plethora of other evidence would indicate this finding to be sound. However, one would not have expected the depicted decrease in daily growth until matric suction exceeded 1.0, or possibly, 1.5 bars. But, the equation required the curve to be a parabola. The decrease in daily growth at values

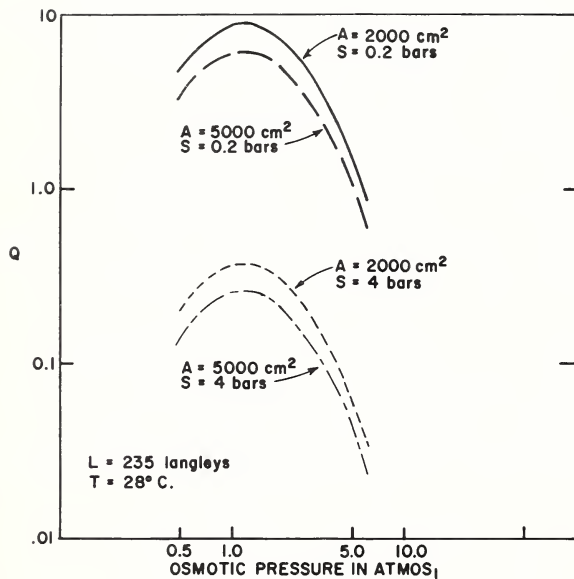


Figure 66

Change in relative growth as affected by calculated
osmotic pressure

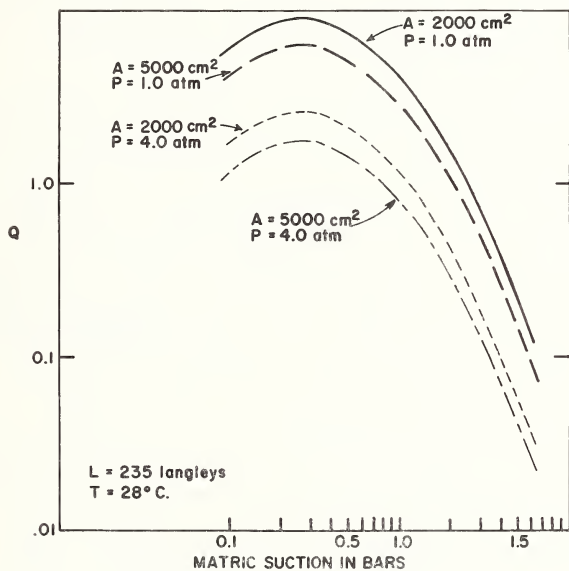


Figure 67

Change in relative growth as affected by matric suction

of matric suction below 0.3 bars may be easily rationalized. As the larger soil pores become filled with water at low soil moisture tensions, oxygen supply to the absorbing roots is impaired. The negative effect of low moisture tension in the wet cultures was much in evidence in most quantitative characterizations of the data.

As will be emphasized later, it is imperative to keep in mind that there was a high degree of intercorrelation between values for osmotic pressure and matric suction. For example, values of 0.5 atmos osmotic pressure only occurred in the "no" salt cultures when these contained sufficient water to lower soil moisture tension to 0.1 bars. As water content of the soil decreased, both osmotic pressure and matric suction increased. Actually, in the regression equations used, there was no way for the computer to effectively differentiate between the effect of osmotic pressure and matric suction. Under most programs for multiple regression analysis, the computer assigns a maximum of variance to the dominant independent variable even though there is intercorrelation between independent variables. Throughout the various approaches used in this study, salinity is the dominant independent variable.

The trends in Figures 66 and 67 may be more critically examined by conversion to a linear scale as shown in Figure 68. The locus of the curve for "W vs P" appears reasonable except for the inferred evidence that the downward trend at the left is reflecting oxygen deficiency and not the effects of a

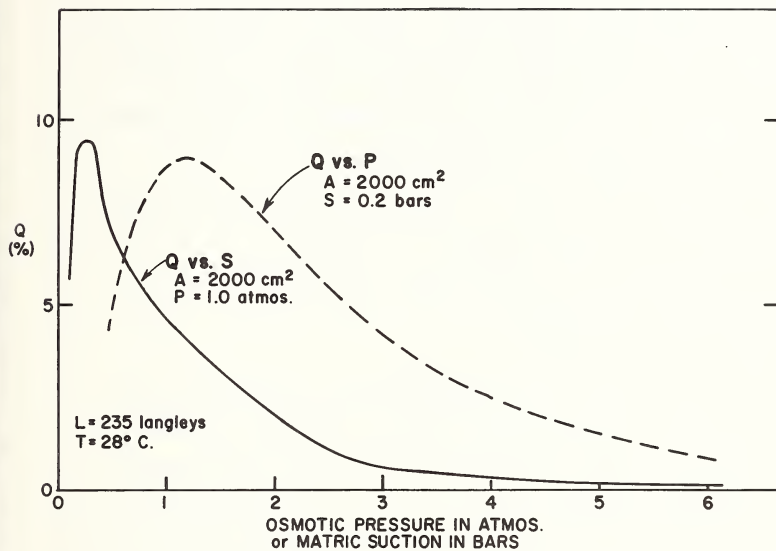


Figure 68

Change in relative growth as affected by a component of the
 soil moisture stress

decrease in osmotic pressure of the soil solution. The locus of the curve for "Q vs S" is feasible between 0.1 and 0.3 bars; but one might well have anticipated that the curve be essentially invariant at a maximum level between 0.3 and 1.5 bars; that is, the precipitous drop in this curve between 0.3 and 2.0 bars does not appear to represent reality. There is a good case to suppose that this apparently anomalous locus is reflecting the constraints of a parabolic function between $\ln Q$ and $\ln S$ together with interaction with values for $\ln P$.

Several attempts were made to modify equation [37] using Hoerl's discussion of curves and their equations to find functions that might more effectively express the relationships between $\ln Q$ and environmental inputs.

Unfortunately, every trial resulted in relationships for the pooled data that carried higher values for the standard error of estimate and lower values for the index of determination, R^2 . Consequently, this effort was rather disappointing, and there is no point in wallowing through these negative findings.

One must conclude that this approach using Fisher's Relative Growth Function has great possibilities for studying plant growth in relation to an array of varying environmental factors. It is essential that the quantitative expression relating Fisher's Function to an environmental factor must be of a mathematical form that in some degree would approach empirical reality. That is, one must avoid a poor mathematical characterization of key environmental inputs so that a low index of multiple correlation results in spurious concomitance with environmental factors having little actual impact.

It is remarkable that in the analysis of data on evapotranspiration (Table 13), light and temperature had consistent effects on rate of water loss from the plants. The findings in Table 57 seem to imply that aerial environment had little consistent effect on relative growth as compared to the physico-chemical status of the soil substrate. One may validly explain the foregoing by conceding that neither equations [12] nor [37] adequately portray the actual relationships between environmental factors and relative growth. Further analyses were warranted.

Effect of Leaf Position. The previous section related change per day in total leaf area with environmental conditions. It is of interest to explore possible changes in relative leaf growth as affected by environment at different positions of the leaves on the plants. The data for calculated leaf area for each successive pair of leaves up the stem in each treatment were pooled and the relation of relative growth to environmental inputs ascertained by an equation analogous to [12] after adjustment for the change in relative growth with change in total leaf area on the "no salt-wet" treatment similar to use of equation [36]. It would be superfluous to report all data for all leaf parts. A sufficient indication of the findings may be gained by merely reporting the data for the first and fourth pair of leaves on each plant in each treatment. The values for the derived coefficients are shown in Table 58. For the "OS-W" plants, most all of the variance in $\ln Q$ was removed by the relationship with leaf area, and the residual variance had no relation to environmental input. Since the first leaves on the "OS-D" were essentially under the "OS-W" treatment at the time of their growth, the effect was the same as for "OS-W" plants.

The effect of light was quite consistent in that it was found to have essentially no effect.

Added salt had a consistently negative effect on relative growth of both sets of leaves, but the magnitude of the effect varied considerably. Note the positive coefficient for "P" on the fourth leaves of the "OS-D" treatment. No explanation for this seemingly erratic behavior is offered.

Table 58

Coefficients for relative growth (Q) of leaf pairs with environmental factors using logarithmic form of equation [12]

Treatment	Leaf Pairs	Coefficients				R ²	S.E.
		ln L	ln T	ln P	ln S		
OS-W	1st	.125	-.512	-.109	.099	.014	.363
	4th	.009	.328	.31	-.082	.059	.186
OS-D	1st	.677	-1.379	-.044	-.356	.085	.887
	4th	.028*	-.267**	.751***	-.731***	.652	.779
MS-W	1st	-.517	-.298***	-4.825**	1.628**	.553	.868
	4th	.180	-1.624**	-8.975	2.414***	.588	.845
MS-D	1st	-.501	1.565***	-12.648***	2.679***	.926	.410
	4th	-.046	-2.787***	-10.727***	1.845***	.784	1.143
HS-W	1st	-.709	.126***	-4.688***	-.411*	.872	.568
	4th	.200	-1.195	-2.990***	.129	.697	.894
HS-D	1st	-.433*	.683***	-6.199***	-.703***	.949	.416
	4th	.312*	-1.862**	-2.750***	-.013	.799	.981

*Probability = .05

**Probability = .01

***Probability = .0001

The coefficients associated with matric suction varied unduly from negative to highly positive values. This would appear to be unrealistic.

The coefficients related to temperature had in most cases a high degree of significance, but the magnitude of the coefficients varied considerably. They were always negative for the fourth leaves of the salinized plants; and tended to be positive for the first leaves of said plants.

Before attempting to draw too many conclusions from Table 58, it would be advantageous to consider Table 59, showing simple correlation coefficients between input variables and $\ln Q$ as well as intercorrelations between $\ln L$ and $\ln T$, and $\ln P$ and $\ln S$. It is fundamental to note that the intercorrelation coefficients between values for light and those for temperature averaged about 0.68 and were all very highly significant; and the coefficients for the intercorrelation between values for osmotic pressure and those for matric suction averaged 0.97. This situation is basic to an attempt to interpret Table 58 showing the coefficients derived from the multiple regression program. As emphasized previously, the computer allocates a maximum of variance in the dependent variable to the dominant independent variable. Thus, any actual effect that light may have had on $\ln Q$, would tend to appear in the regression on temperature. Because of the very high degree of intercorrelation between osmotic pressure and matric suction, most of the variance in $\ln Q$ will be associated with $\ln P$ rather than $\ln S$ in multiple regression even though this may not be reality. Obviously, both osmotic pressure and matric suction vary inversely with water content of soil. Hence, most all of the

Table 59

Correlation coefficients between $\ln Q$ and \ln of inputs, together
relation between $\ln L$ and $\ln T$, and $\ln S$

Treat- ment	Leaf Pairs	$\ln Q$ vs $\ln L$	$\ln Q$ vs $\ln T$	$\ln Q$ vs $\ln P$	$\ln Q$ vs $\ln S$	$\ln L$ vs $\ln T$	$\ln P$ vs $\ln S$
OS-W	1st	-.010	-.092	.106	.062	.691***	.964***
	4th	.141	.206	-.116	-.096	.695***	.938***
OS-D	1st	.033	-.058	-.170	-.177	.667***	.985***
	4th	.200	.088	-.580***	-.640***	.625***	.980***
MS-W	1st	-.193	-.145	-.229	-.322*	.633***	.952***
	4th	-.064	-.198	-.327*	-.333*	.627***	.987***
MS-D	1st	-.348*	-.186	-.897***	-.848***	.642***	.975***
	4th	-.088	-.009	-.725***	-.725***	.677***	.987***
ITS-W	1st	-.346*	-.264	-.719***	-.641***	.610***	.968***
	4th	-.110	-.142	-.261*	-.374**	.777***	.975***
ITS-D	1st	-.377**	-.247	-.887***	-.886***	.668***	.977***
	4th	-.017	-.068	-.540***	-.539***	.836***	.997***

*Probability = .05

**Probability = .01

***Probability = .0001

most all of the effect of decreasing soil water percentage appears in the coefficient for $\ln P$ in Table 58. The coefficients for $\ln S$ represent a relation to the fringe variance in $\ln Q$ after the effect of $\ln P$ has been removed. Thus, the coefficients for $\ln S$ in Table 58 may be quite unrealistic except in the "OS-D" treatment. Also, one cannot avoid having doubts about the findings presented in Table 57 involving the quantitative effect of $\ln P$ and $\ln S$.

Effect of Leaf Age. The data for daily increase in calculated leaf area for each leaf up the stem of each plant was segregated into time periods constituting one-third of the time for most of the growth on each leaf to take place. For the "control" plants, most all of the growth for each leaf took place in 21 days. On some of the plants under soil moisture stress, growth of a leaf often required 30 days. The data for each leaf pair up the stem for each plant in a treatment was pooled, thereby providing at least 28 observations for a growth period on a given pair of leaves from two plants.

The data attained are just too voluminous to report in toto. The findings may be adequately indicated by showing only the results for the third pair of leaves on each plant under each treatment.

Analysis of the data was the same as the procedure used in the previous section, except for the segregation into leaf periods and the use of a single formula for adjusting for the effect of leaf area by pooling data for all three periods on the "OS-W" plants.

The first period is the time of initial expansion, the second period that of major expansion, and the third period is largely associated with maturation.

The data in Table 60 show that the main consistent relationship was between $\ln Q$ and $\ln P$ in the salinized treatments: the coefficients were all negative and all of appreciable magnitude. There was considerable range in the size of the coefficients, but no consistent trend related to period of leaf growth.

Table 60

Regression coefficients between $\ln Q$ on the logarithms of environmental inputs by leaf periods

Treatment	Growth period	Coefficients				R ²	S.E.
		$\ln L$	$\ln T$	$\ln P$	$\ln S$		
OS-W	1st	.767*	.439	.026	-.058	.243	.277
	2nd	.126	.740*	.071	-.074	.243	.222
	3rd	-.138	2.184	-.181	.151	.216	.389
MS-W	1st	-.121*	-.159	3.351***	.762**	.522	.283
	2nd	.103	-.518	-9.667***	2.703***	.845	.491
	3rd	-.105	-.071	-2.129***	-.042	.852	.351
HS-W	1st	-.237	-1.118**	-.411***	.042	.881	.241
	2nd	.252	-1.008***	-3.751***	-.068	.904	.509
	3rd	-1.435	4.231***	-4.830***	.378*	.952	.623
OS-D	1st	-.021	.287**	.111	-.298***	.685	.290
	2nd	-.388	-1.967***	1.116***	-1.268***	.911	.522
	3rd	.102***	2.611***	1.448***	-1.218***	.932	.702
MS-D	1st	-.105***	-.071***	-2.129***	-.042	.852	.351
	2nd	-.336*	1.910***	-9.492***	1.752**	.782	1.074
	3rd	-.475	-.157***	-18.779***	3.941***	.979	.551
HS-D	1st	-.200***	.447***	-1.480***	-.370*	.942	.272
	2nd	-.300***	.067***	-3.330***	-.193	.915	.834
	3rd	-.653***	.530***	-6.362***	.545*	.952	.913

*Probability = .05

**Probability = .01

***Probability = .0001

The regression coefficients relating $\ln Q$ to $\ln S$ by growth periods within treatments were quite erratic. As evident in Table 61, the inter-correlation between $\ln P$ and $\ln S$ was exceedingly high. As stated previously, both were inversely related to the water content of the soil. Thus, the computer program allocated most of the variance in $\ln Q$ to concomitant variance in water content of soil as indicated by $\ln P$. Thus, the relation between $\ln Q$ and $\ln S$ in Table 60 show the fringer effects of variation in $\ln Q$ and soil moisture percentage. The high degree of comparability of the correlation coefficients for $\ln Q$ vs. $\ln P$ and $\ln Q$ vs. $\ln S$ in Table 61 attest to the probable distorting in the allocation of variance in $\ln Q$ between $\ln P$ and $\ln S$.

These results case doubt on any multiple regression analysis wherein $\ln P$ and $\ln S$ are treated as "supposedly independent" variables. A different approach was deemed to be in order.

Table 61
Correlation Coefficients

Treatment	Growth Period	ln Q vs ln L	ln Q vs ln T	ln Q vs ln P	ln Q vs ln S	ln L vs ln T	ln P vs ln S
OS-W	1st	.399*	.190	-.266	-.242	.067	.980***
	2nd	-.033	.353	-.144	-.134	-.308	.977***
	3rd	.231	.448*	.006	.130	.641**	.948***
MS-W	1st	-.115	-.057	-.442**	-.370*	.115	.963***
	2nd	.036	-.178	-.383*	-.357*	-.258	.983***
	3rd	.294	.259	-.369*	-.323	.926***	.984***
HS-W	1st	-.016	-.531**	-.540**	-.493**	-.105**	-.975***
	2nd	.004	-.176	-.621**	-.664***	.762***	.968***
	3rd	-.314	-.047	-.504**	-.596**	.816***	.976***
OS-D	1st	-.345	-.358*	-.700***	-.776***	.053	.962***
	2nd	.228	-.170	-.845***	-.893***	-.240	.983***
	3rd	.288	.415*	-.853***	-.843***	.923***	.976***
MS-D	1st	.113	.510**	-.741***	-.824***	-.046	.964***
	2nd	.195	.257	-.786***	-.806***	.564**	.989***
	3rd	-.152	-.036	-.900***	-.863***	.842***	.988***
HS-D	1st	-.236	-.148	-.625**	-.635***	-.112	.997***
	2nd	-.004	.032	-.751**	-.767***	.916***	.997***
	3rd	-.260	-.290	-.725***	-.700***	.564**	.998***

*Probability = .05

**Probability = .01

***Probability = .0001

Recapitulation

In order to approach a more acceptable rationale for depicting the quantitative relationship between pertinent environmental factors and foliar expansion on these castor beans, certain findings from preceding sections ought to be taken into account:

1. Due to the very high intercorrelation between values for $\ln P$ and $\ln S$, one may not ascertain a differentiation of the real effects of these two factors in a conventional multiple regression analysis. To cope with this difficulty, an alternate approach should be followed. Selected data may be used to obtain a more rational relationship between relative growth and osmotic pressure, or with matric suction. The derived relation may then be locked into the multiple regression equation analogous to the procedure used with the relation between relative growth and total leaf area.

2. At low values of matric suction, less than 0.15 bars, one might have anticipated that impaired soil aeration would adversely affect the absorbing cells of the roots. Roots with impaired metabolic status may lose their capacity to selectively exclude sodium (4, 31). There was evidence to support this possibility in the data of Table 39. Thus, if there is a definite interaction between the effect of salt level and the effect of poor soil aeration due to high soil moisture content, the pooling of all data in the "wet" series of cultures to attain the composite effect of low soil moisture tension on relative growth would be of questionable validity.

3. There was a high degree of intercorrelation between values for $\ln L$ (light), $\ln T$ (temperature), and $\ln H$ (humidity). Since these attributes of the aerial environment were not experimental inputs, but varied at random, a fully satisfactory means of adequately segregating their specific effects on the probable prevalence of water deficits within the plant may not evolve from the multiple regression analyses employed. There was much evidence in preceding sections of this report that elevated temperature had an adverse effect on relative growth in the salinized cultures. These observations on the effect of increasing aerial temperature are more probably the effect of increasing diffusion pressure deficit (DPD) of the ambient air and the consequent effect on internal water deficits. The derived relations of relative growth to temperature under enhanced soil moisture stress may also be reflecting in some degree the effect of elevated solar radiation and low relative humidity on the DPD of the ambient air. Consequently, the procedure of pooling treatments to obtain the composite effect of aerial attributes on relative growth may be of questionable validity. There is also the possibility that the relationship between $\ln Q$ (relative growth) and other environmental inputs may not be linear.

4. Ascertaining the osmotic effect on water availability to the absorbing roots by calculating average osmotic pressure from known salt content and known water content is definitely a questionable procedure. Upon irrigation, either surface or subsurface, there will be a pocket of soil essentially free of salt in the soil water. Roots will preferentially

absorb this water. Thus, immediately following an irrigation, the salinized plants were undoubtedly responding to an essentially non-saline soil status. As water enters the roots during an irrigation interval, much of the salt will be excluded by roots of non-halophytic plants. Salt may accumulate at the surface of the absorbing roots. These postulations have supporting evidence in Figure 60.

Proceeding as indicated under stipulation #1, above, data from the "dry" series of cultures were partitioned so as to segregate those data that prevailed when the daily values for matric suction were between 0.25 and 0.75 bars under the assumption that matric suction in that range would have little adverse effect on plant growth. These data were then used to determine the net effect of the values for osmotic pressure on values for relative growth ($\ln Q^1$) that had been adjusted for the effect of total leaf area on $\ln Q$. Values for $\ln P^{1/}$ ranged from -1.23 to 0.96. Plotting the raw data (Figure 69) showed the relation to be quite linear for each salt level between values of -1.23 and 0.7 for $\ln P$. Above 0.7, the relation dipped very sharply as though some terminal value of $\ln P$ was being approached asymptotically.

The raw data showed that whenever the calculated value for osmotic pressure of the soil solution approached 6.8 atmos., relative growth approached zero. Hence, 7.0 atmos. was taken as the asymptote mentioned in the preceding paragraph. The $\ln P$ value for 7.0 atmos. is 0.99; so unity was taken as the asymptote of $\ln P$. The relation

$\frac{1}{\ln P} = \ln \left(\frac{P_o}{M_{P_o}} \right)$, where P_o is the calculated value for osmotic pressure, and M_{P_o} is the mean of all P_o values.

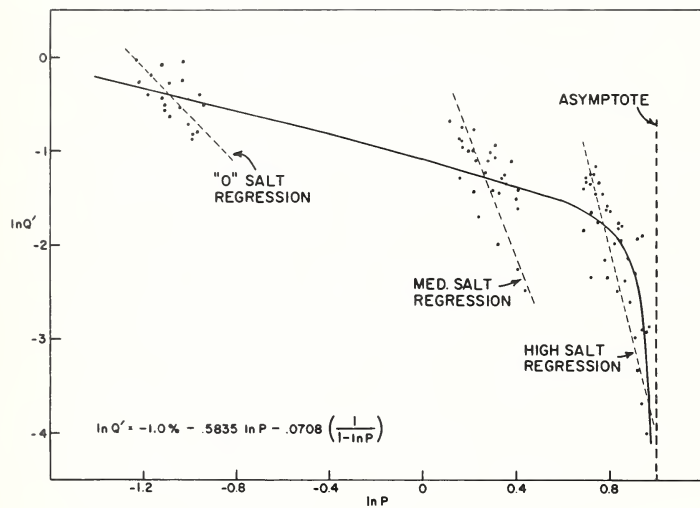


Figure 69

Relation between $\ln Q'$ and $\ln P$ for daily values of matric suction within the limits of 0.25 bars to 0.75 bars

between $\ln Q^1$ was expressed as:

$$\ln Q^1 = K^1 + a \ln P + b \left(\frac{1}{1 - \ln P} \right) \quad [38]$$

where $\ln Q^1 = \ln Q$ values corrected for effect of leaf area (Equation [11]), and $K^1 =$ adjustment to K of equation [36].

Figure 69 shows the relation obtained for the data used as well as the constants derived for equation [38]. The standard error of estimate, S.E., for this relation was found to be 0.388; and the index of determination, R^2 , was 88.8%. The dispersion of the data in Figure 69 indicates why the S.E. was relatively high. It was also noteworthy that the regressive trends in the data at different salt levels were somewhat transverse to the general relationship, excepting at the high salt level wherein the asymptotic trend of the general relationship approach the linear relation specific for the "high salt" data. This divergence in regression trends suggests that the spread in calculated values for $\ln P$ within each salt level was inadequate for the spread in values for $\ln Q^1$ if the general regression curve shows the true relation between $\ln Q^1$ and $\ln P$. This finding leads to the same conclusion as the discussion of Figure 60; viz., the calculated values for average osmotic pressure in the soil solution were inadequate for characterizing the osmotic pressure of the soil water actually being absorbed by a given portion of the roots on a given day.

As indicated in stipulation #4 above, there was ample basis for a rationale that the calculated values for average osmotic pressure should be adjusted downward or upward on a given day for a better index of effective osmotic pressure of the soil solution. For example,

on the day when a given culture was irrigated with Riverside tap water having an osmotic pressure of 0.12 atmos., there would be a pocket of soil water in the container approaching this low level of O.P. However, in order to be conservative, the adjusted minimum O.P. values in column III of Table 62 were arbitrarily chosen as a modest downward adjustment of the calculated minimum O.P. values in column I. Thus, Figure 60 indicated that a probable minimal value for adjusted O.P. in the MS-D cultures was 1.1 atmos. Yet, the actual value selected was 1.4 atmos. (column III). Further, Figure 60 implied that the minimal value for adjusted O.P. on the HS-D cultures was 2.2 atmos. But 2.6 atmos. was selected as the adjusted minimum O.P. for these cultures.

Figure 60 indicated the cultures in both the MS-D and HS-D treatments attained maximum adjusted O.P. values of 12 atmos. One recalls that the MS-D cultures were allowed to dry to a much lower level of soil moisture content than the HS-D cultures, thereby accounting for the apparent similarity in salt effects at the adjusted maximum O.P. To be conservative, the adjusted maximum O.P. in both the MS-D and HS-D treatments was arbitrarily selected as 9.8 atmos. as shown in column IV of Table 62.

Columns V, VI, VII, and VIII show the derived values for minimum and maximum $\ln P$ and minimum and maximum "adjusted" $\ln P$. The latter term is hereinafter designated as $\ln P_a$.

Columns IX and X show the regression coefficients for the linear regression between $\ln P$ and $\ln P_a$.

Table 62

Adjustment of calculated values of osmotic pressure of the soil solution in the various treatments and the coefficients of linear regression used in making the adjustment

Treatment	I	II	III	IV	V	VI	VII	VIII	Regression Coefficients		O.P. at which adjustment makes no change
	Min. O.P.	Max. O.P.	Min. O.P.	Adjust. Max. O.P.	Min. In P	Max. In P	Adjust. Min. In P _a	Adjust. Max. In P _a	$\frac{IX}{a}$	$\frac{X}{b}$	
	atm.		atm.		atm.						
OS-W	0.50	0.80	0.30	1.10	-1.649	-1.179	-2.159	.860	2.39	2.76	0.67
MS-W	2.00	2.80	1.40	3.50	-0.262	.074	-.632	.307	.10	2.79	2.46
HS-W	3.40	4.50	2.60	5.50	.268	.549	0.0	.751	-.736	2.71	4.00
OS-D	.50	1.40	.30	2.00	-1.649	-.619	-2.160	-.272	.861	1.83	0.92
MS-D	2.00	5.20	1.40	9.80	-.262	.693	-.632	1.325	-.113	2.08	2.94
HS-D	3.40	6.70	2.60	9.80	.268	.947	0.0	1.325	-.885	2.32	5.08

That is, in the OS-W treatment:

$$\ln P_a = 2.39 + 2.76 \ln P \quad [39]$$

Column XI shows the value for adjusted O.P. that exactly coincides with the value for calculated O.P. It may be noted that these latter values are intermediate between the minimum and maximum values.

In setting up equations to evaluate environmental effects within each treatment, it was found to be desirable to characterize the general relationships between Fisher's "relative growth" and accumulated leaf area in a different manner than that followed in equation [36] and illustrated by Figure 66. The equation used was:

$$Q_A = K (A^1)^b e^{c (A^1)^2} \quad [40]$$

Where Q_A = "relative growth" rate, calculated from accumulated leaf area; $A^1 = A/1000$; i.e., accumulated leaf area in cms^2 divided by 1000; and K, b, c = constants.

Equation [40] is a slight modification of equation [11]. In the logarithmic form equation [40] becomes:

$$\ln Q_A = \ln K + b \ln A^1 + c (A^1)^2 \quad [41]$$

Table 63 presents the values for the coefficients used in the application of equation [41] on the data from each treatment.

The first objective of this section (Recapitulation) will be to obtain a more rational characterization of the relation between matric suction and relative growth rate in the "no salt" cultures wherein the variation in concentration of soil solutes have minimal effect. To do this, the linear regression of $\ln Q$ on $\ln P_a$ was ascertained for the OS-W and

Table 63

Constants used in equation [40] for each treatment used to calculate values for $\ln Q_A$. Respective values for S.E. and R^2 are also provided

Treatment	$\ln K$	b	c	S.E.	R^2 %
OS-W	2.702	-.4028	-.00684	.1711	97.6
MS-W	2.230	-.4606	-.00219	.1100	98.0
HS-W	1.766	-.4551	+.0116	.1290	93.9
OS-D	2.458	-.6324	-.00706	.3210	89.7
MS-D	1.252	-1.110	+.0789	.710	60.2
HS-D	.936	-.7014	+.0463	.445	70.5

OS-D treatments, respectively; and then these regressions were locked into the mathematical model relating growth to environmental effects.

For the OS-W treatment the latter regression coefficient was found to be -0.201 and for the NS-D treatment, -0.480.

For the OS-W plants,

$$\ln Q_A = 2.702 - .4028 \ln A^1 - .00684 (A^1)^2 \quad [41]$$

$$\ln Q^1 = \ln Q - \ln Q_A \quad [42]$$

where $\ln Q^1$ values are the resultant of correcting the raw values for $\ln Q$ with the calculated values of $\ln Q_A$ derived from equation [41].

The mean of all derived $\ln Q^1$ values was found to be zero.

Osmotic pressure values were adjusted as indicated previously; i.e.,

$$\ln Pa = 2.39 + 2.76 \ln P \quad [39]$$

Let $\ln Q^1_p$ be the corrections in $\ln Q$ after adjustment by equation [40] and by the impact of $\ln Pa$ having the regression coefficient of -0.201 on $\ln R^1$. Thus,

$$\ln R^1_p = \ln R^1 - .201 \ln Pa - M_{\ln Pa} \quad [43]$$

where $M_{\ln Pa}$ is the mean of all $\ln pa$ values used in the OS-W treatment.

Then,

$$\ln Q'' = \ln Q^1_p \quad [44]$$

wherein the $\ln Q''$ values are those for relative growth rate after adjustment for accumulated leaf area and the adjusted osmotic pressure values.

In the OS-W cultures, the effects of light, temperature, and matrix suction were evaluated by the following multiple regression equation:

$$\ln Q'' = \ln K'' + a \ln L + b (\ln L)^2 + c \ln T + d (\ln T)^2 + e \ln S + f (\ln S)^2 \quad [45]$$

where $\ln K''$, a , b , c , d , e , and f are constants.

It was assumed that the regression of $\ln Q''$ on $\ln L$, $\ln T$, and $\ln S$ might be non-linear, so terms for second degree effects were included.

For the OS-D plants,

$$\ln Q_A = 2.458 - .6324 \ln A' - .00706 (A')^2 \quad [46]$$

$$\ln Q' = \ln Q - \ln Q_A \quad 42$$

The mean of all derived $\ln Q'$ values was found to be zero.

Osmotic pressure values were adjusted by

$$\ln P_a = 0.861 + 1.83 \ln P \quad [47]$$

Regression of $\ln Q'$ on $\ln P_a$ was found to be -0.480 .

Corrections of $\ln Q'$ for osmotic pressure effects was determined by:

$$\ln Q_p = \ln Q' - (-0.480) (\ln P_a - M_{\ln P_a}) \quad [48]$$

$$\ln Q'' = \ln Q'_p \quad [44]$$

The effects of light, temperature, and matric suction were evaluated by the following multiple regression equation:

$$\ln Q'' = \ln K'' + a \ln L + b (\ln L)^2 + c \ln T + d (\ln T)^2 + e \ln S + f (\ln S)^2 + g S^2 \quad [49]$$

where $\ln K''$, a , b , c , d , e , f , and g are constants.

Table 64 presents the constants derived for the OS-W and OS-D plants by use of equations 45 and 49. The low value for $R^2 - 23.7\%$ - showing the variance accounted for in $\ln Q''$ by use of equation [45] may seem unduly low. However, it must be borne in mind that 97.6% of the

Table 64

Constants derived by use of equations [45] and [49]

Coefficient	OS-W	OS-D	Environmental effect evaluated
	Equation [45]	Equation [49]	
ln K	.0706	.2582	
a	.1037***	.2198**	Light
b	.0232	.1932	
c	.2213	-.5067*	Temperature
d	-.5220	-1.9876*	
e	.0406**	-.1989***	Matric suction
f	-.0432	-.1967***	
g		.0358**	
S.E.	.152	.346	
R ² (%)	23.7 ^{1/}	57.9 ^{2/}	

^{1/}Significant probability exceeds .001

^{2/}Significant probability exceeds .0001

variance in $\ln Q$ -- Table 63 -- was accounted for by concomittant variance in accumulated leaf area. That is, there was little residual variance -- 2.4% -- in values for $\ln Q$ after removal of that due to leaf area. Table 64 shows that 23.7% of this residual variance was associated with concomittant variance in environmental effects. Nevertheless, significance of the latter regression exceeded a probability of 0.001. The high significance of coefficient "a" indicates that increasing level of daily solar radiation increased relative growth rate for the OS-W plants. Also, the high significance of coefficient "e" indicated that increasing matric suction of the soil from 0.08 to 0.3 bars was associated by an increase in relative growth rate for these same plants. This is shown in Figure 70. This latter point may be more properly stated in that it infers that poor soil aeration associated with the lower levels of matric suction that prevailed impaired relative growth rate.

Within the OS-D treatment, 57.9% of the variance in $\ln Q$ was associated with concomittant variance in the environmental variables specified. Since 89.7% of the variance in $\ln Q$ (Table 63) was associated with variance in accumulated leaf area, the value of 57.9 associated with residual variance in $\ln Q$ is remarkably good. Increasing level of daily solar radiation was definitely associated with increased relative growth rate; but increasing level of maximum daily temperature appeared to have a depressing effect on the growth. It is reasonable to expect that plants subjected to intense soil moisture depletion would be adversely affected by elevated temperature.

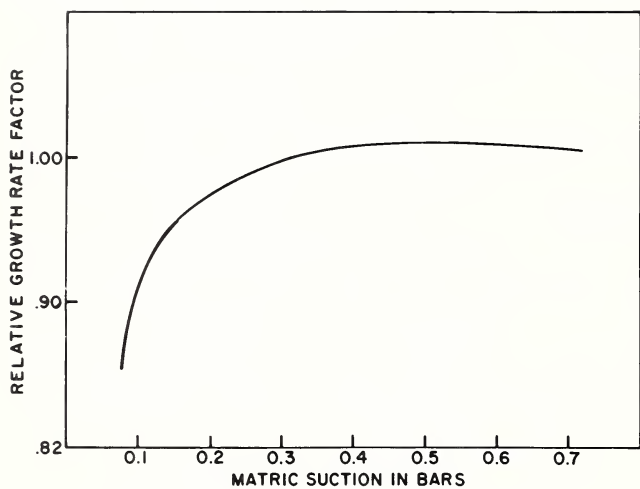


Figure 70

Change in relative growth rate with change in matric suction at low values of matric suction

All of the three terms expressing the complex relation between the growth function and level of matric suction were found to be highly significant in the OS-D treatment. The relation derived from use of coefficients "e," "f," and "g" from Table 64 is shown in Figure 71. This curve indicates that between 0.08 and 0.2 bars of matric suction, relative growth rate increased; between 0.2 and 2.5 bars, there was a rapid decrease in this rate; and between 2.5 and 5.0 bars, the rate of relative growth decreases rather moderately. One can readily rationalize that this picture of the effect of increasing matric suction on the growth of vigorously vegetative plants is reasonably valid.

The next step in the "recapitulation" procedure was that of taking the regression coefficients "e" and "f" of Table 64 and locking them into regression equations for the three levels of salinity treatment in the "wet" series of cultures, while regression coefficients for the effects of light, temperature, and adjusted osmotic pressure on relative growth rate were computed. That is, the coefficients in equation [50] were determined:

$$\ln Q = \ln K + a \ln L + b (\ln L)^2 + c \ln T + d (\ln T)^2 + e \ln P_a + f (\ln P_a)^2 \quad [50]$$

Just as an approximated regression coefficient (see equation [43]) for the effect of osmotic pressure was locked into the computation of equation [45], the following effect of matric suction was locked into equation [50]:

$$\ln Q'_s = .0406 \ln S - .0432 (\ln S)^2 \quad [51]$$

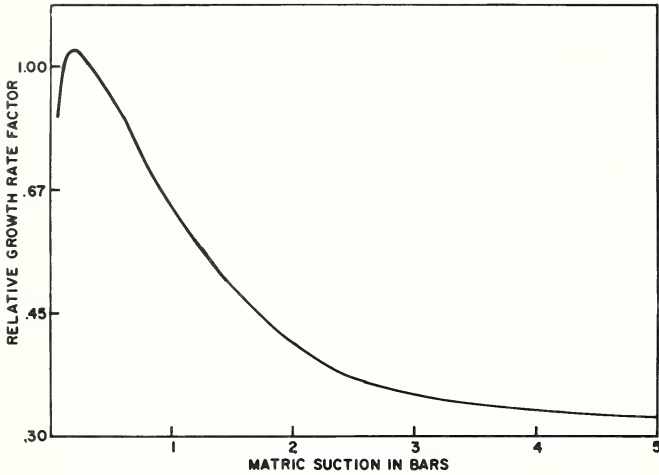


Figure 71

Change in relative growth factor with change in matric suction over a wide range of values for matric suction

Equation [51] was applied after adjusting for the effects of accumulated leaf area using the coefficients from Table 63.

In the "dry" series of cultures, the effects of the three levels of salinity were evaluated by locking into the computer the effect of matric suction shown in Figure 71 and deriving the constants for the following regression equation:

$$\begin{aligned} \ln Q'' = \ln K'' + a \ln L + b (\ln L)^2 + c \ln T + d (\ln T)^2 + e \ln P_a \\ + f (\ln P_a)^2 + g P_a^2 \quad [52] \end{aligned}$$

After correcting the primal $\ln Q$ values for the effects of accumulated leaf area by use of proper constants in equation 40 (Table 63), the derived $\ln Q'$ values were adjusted for the effects of matric suction by equation 53 :

$$\ln Q'_s = -.1989 \ln S - .1967 (\ln S)^2 + .0358 S^2 \quad [53]$$

The derived values for the coefficients in equations [50] and [52] are given in Table 65. Adjusted osmotic pressure values had a highly significant but negative effect on relative growth rate on all treatments. One must keep in mind that these regression coefficients for the effects of osmotic pressure pertain to deviations from the mean adjusted osmotic pressure within each treatment and in no way reflect osmotic effects between treatment means such as those shown by the displacement of curves in Figure 66.

Figure 72 shows the trends for variation in $\ln Q''$ at various applicable values of $\ln P_a$ for the six treatments using the appropriate

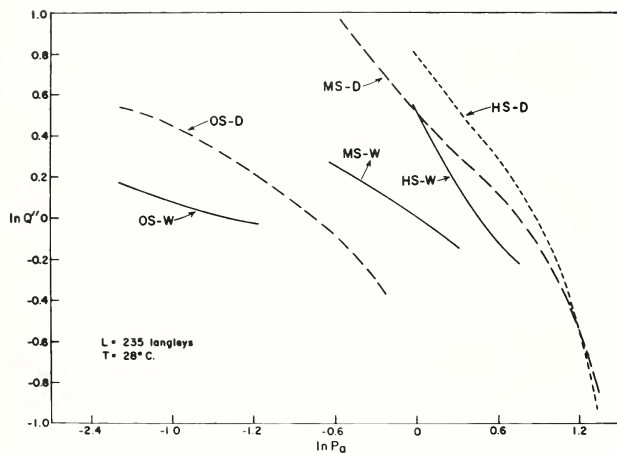


Figure 72

Relation between $\ln Q'$ and $\ln P_a$ in the various treatments

Table 65

Regression coefficients derived by use of equations [50] and [52]

Coefficient	Equation [50]		Equation [52]		Environmental effect evaluated		
	OS-W	MS-W	HS-W	OS-D		MS-D	HS-D
In K"	-.1725	-.0001	.5189	-.7130	.6161	.9358	
a	.0998***	.0916*	-.2677**	.4358***	.2175	.0750*	Light
b	.0206	.0130	-.2505	.3909	-.0490	.2013**	
c	.2236	-.2028	-.0048	-.5895**	-2.0862	-1.6248	Temperature
d	-.5157	-1.4155**	-1.8283	-2.6496**	-3.6011	-2.4482	
e	-.0852***	-.4711***	-1.2741***	-.9656***	-.5327***	-.6311	Adjusted
f	.0327	-.0824	.3932	-.1803***	.4237*	.6040**	osmotic
g				.03444	-.01522	-.02165	pressure
S.E.	.1521	.1673	.2238	.2507	.5296	.2976	
R ² (%)	32.0 $\frac{1}{2}$ /	48.8 $\frac{1}{2}$ /	59.7 $\frac{1}{2}$ /	60.5 $\frac{1}{2}$ /	59.2 $\frac{1}{2}$ /	76.8 $\frac{1}{2}$ /	

*Significant probability equals or exceeds .05

**Significant probability equals or exceeds .01

***Significant probability equals or exceeds .001

 $\frac{1}{2}$ / Significant probability exceeds .0001

coefficients from Table 65. In deriving these curves, light and temperature, respectively, were stipulated as being held at their mean values.

All curves in Figure 72 have a negative trend regardless of the mean level of salinity. The loci of the curves for the "dry" series of cultures imply that within a given treatment, a given change in $\ln P_a$ at the higher levels of this factor is more adverse relative growth than at lower levels. The trend of the curves affected by logarithmic conversion, so the same findings are presented on a linear scale in Figure 73. In view of the fact that these curves were derived from the multiple regression equations for different treatments, they provide a remarkably consistent family of trends. Again, it is essential to keep in mind that these curves show the effect of variation from the mean osmotic pressure for the treatment upon relative growth rate. Thus, there was very little variation from the mean O.P. in the OS-W treatments, so there was little impact on relative growth. Yet, this little impact was highly significant.

There was comparatively little variation from the mean O.P. in the MS-W treatment, and comparatively little impact on relative growth, even though said impact was highly significant.

The adjusted osmotic pressure values varied rather widely from their respective means in the MS-D and HS-D treatments, and there was concomitant wide variation in values for the relative growth rate factors. As one would expect, a comparatively small change in adjusted osmotic pressure immediately following an irrigation was associated with a comparatively large change in relative growth. The converse situation

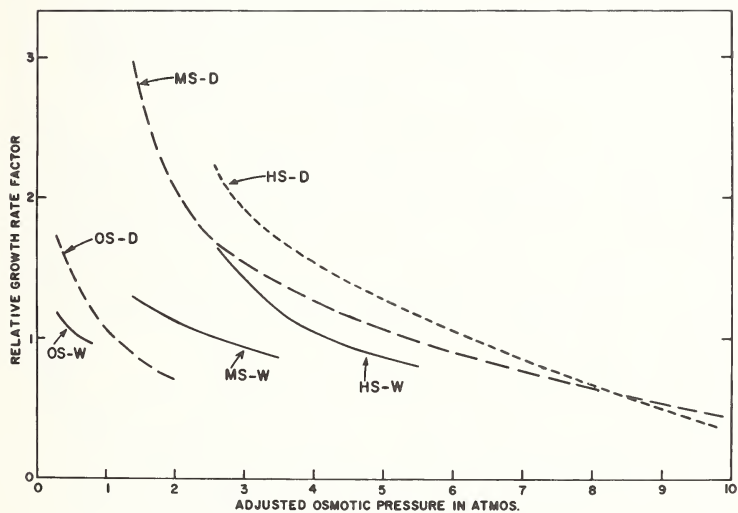


Figure 73

Relation between relative growth factor and adjusted osmotic pressure
in the various treatments

prevailed toward the end of a drying cycle in the MS-D and HS-D treatments. In other words, the loci of the curves in Figure 73 are well within the bounds of what one would expect from the accumulated evidence related to the effect of soil salinity on crop growth. It's of interest that an increase of adjusted osmotic pressure from 3 to 4 atmospheres was associated with reduction in the relative growth rate factor by about 20 percentage units in the HS-W, MS-D, and HS-D treatments.

In every treatment, variations in concentration of the soil solution accounted for a highly significant component of the variance in relative growth rate (Table 65); and it is of interest to consider the extent to which variability in light and temperature was associated with variations in the residual variance.

Solar radiation had a significant effect on relative growth in both the OS-W and OS-D treatments (Table 65). However, the trends of the respective curves were quite divergent as shown in Figure 74. The linear and not the curvilinear component of these two curves attained significance. The much more positive slope for the OS-D curve suggests that increased production of photosynthate under the higher levels of solar radiation may have been advantageous in enabling the OS-D plants better to cope with elevated soil moisture stress.

Figure 75 presents the loci of the curves for the "wet" series of cultures relating solar radiation to relative growth rate. The loci of the curves for the OS-W and MS-W treatments were essentially indistinguishable.

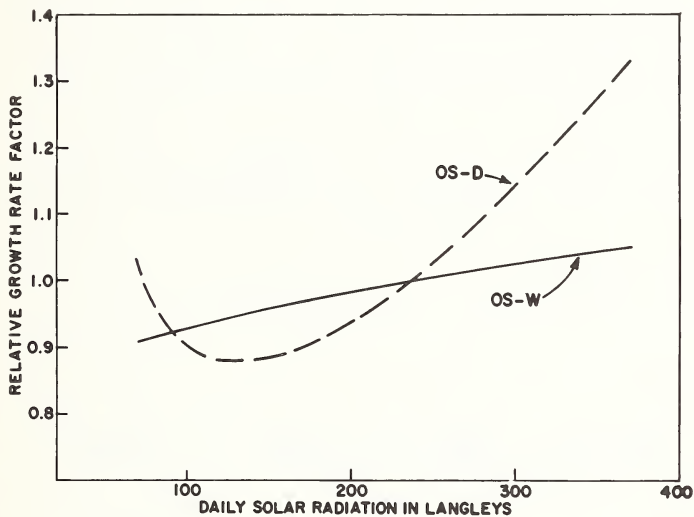


Figure 74

Relation between relative growth factor and solar radiation in the "O"
salt treatments

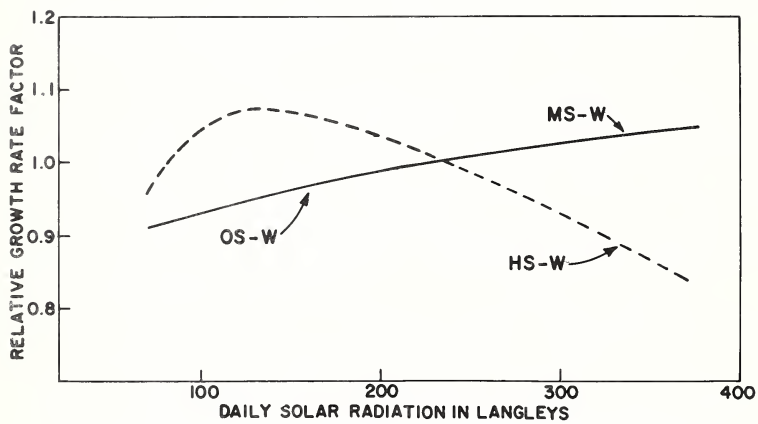


Figure 75

Relation between relative growth factor and solar radiation in the "wet" treatments

The curve for the HS-W plants had a definitely negative trend with only the linear component being significant. There is much evidence that elevated levels of chloride in the substrate have an adverse effect on carbohydrate metabolism. This has been well shown for both potatoes and tobacco. Hence, enhanced solar radiation on the HS-W may intensify internal water deficit. It is important to note the diverging trends of the OS-D curve in Figure 74 and the HS-W curve in Figure 75. In the former, elevated soil moisture stress was mainly due to increased matric suction; whereas in the latter, the higher soil moisture stress was entirely due to salinity.

The trends for the curves relating solar radiation to relative growth rate in the "dry" series of cultures are shown in Figure 76. The curve for the MS-D treatment was of no significance. (This undoubtedly related for the high standard error of estimate -- Table 65 -- found for the MS-D plants). The advantageous effect of high solar radiation on relative growth of the OS-D plants did not prevail for the HS-D plants subjected to the relatively high level of chloride in the substrate.

The effect of maximum daily temperature on relative growth of the unsalinized treatments is shown in Figure 77. The curvilinear components of these two curves are not significant -- Table 65 -- even though the respective regression coefficients for curvilinearity (coefficient "d") are of appreciable magnitude. The locus of the OS-D curve suggests that elevated aerial temperature accentuates internal water deficit in plants subjected to an advanced level of soil moisture depletion.

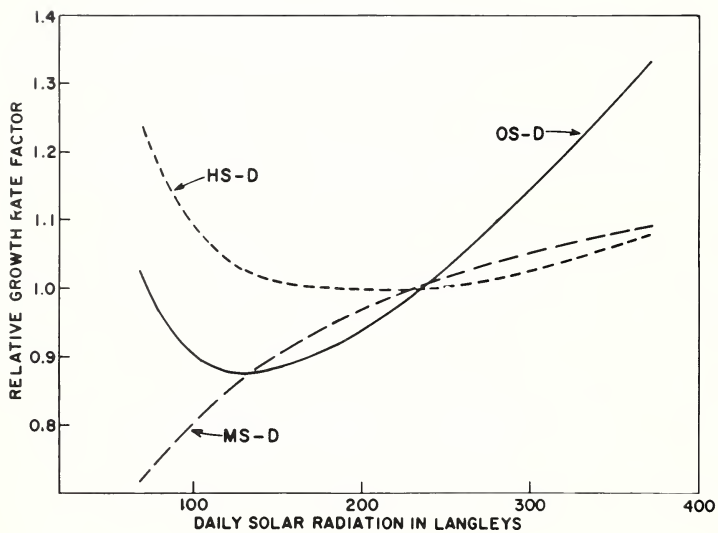


Figure 76

Relation between relative growth factor and solar radiation in the "dry" treatments

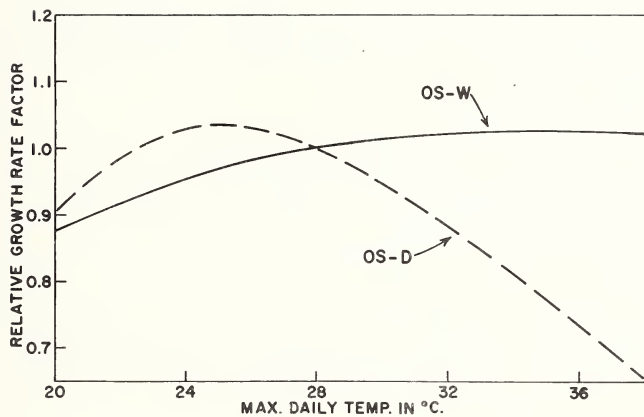


Figure 77

Relation between relative growth factor and maximum daily temperature
in the "O" salt treatments

The curves showing the effect of maximum daily temperature on relative growth in the "wet" series of cultures is shown in Figure 78. Elevated temperature was adverse in the salinized cultures as compared to the control (OS-W). Even though the regression curve for the HS-W plants was not significant, it is of interest that its locus is essentially the same as that for the MS-W treatment. It is common observation that a given level of soil salinity is more adverse to crop growth under a warm climate than under a cool one.

Figure 79 shows the loci of the regression curves in the "dry" series of cultures analogous to the presentation in Figure 78. Plants in all the "dry" treatments were subjected to elevated soil moisture stress, and the effect of increasing maximum daily temperature on relative growth was consistently negative. Even though the curve for the MS-D plants was non-significant, the locus of this curve is very close to that of the HS-D plants. Thus, the trends in Figure 79 are consistent with most experimental findings.

It is concluded that the analysis of the available data presented under this section headed "Recapitulation" is the most satisfactory of any of the approaches attempted in this study. Nevertheless, the standard errors of estimate are shown in Table 65 for each of the six treatments. One could be philosophical and suggest that these S.E. values reveal that the "innate cussedness of protoplasm" was raising its ugly head. Yet, there remains the haunting suspicion that environmental effects were inadequately characterized by the data used in the multiple regression

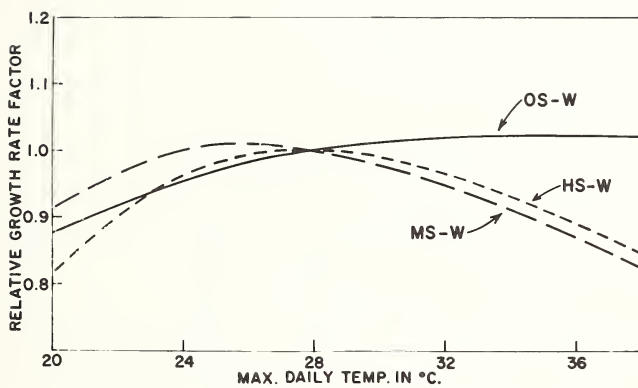


Figure 78

Relation between relative growth factor and maximum daily temperature
in the "wet" treatments

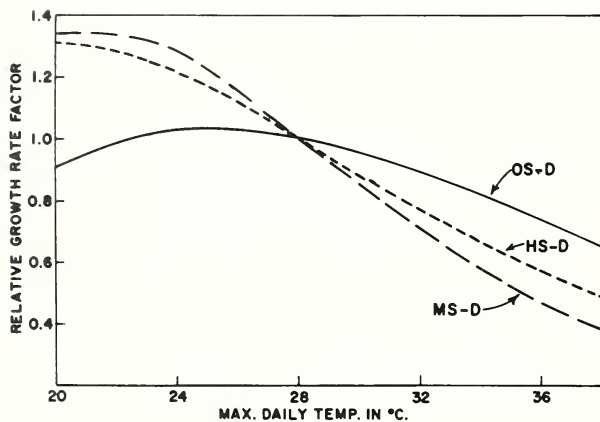


Figure 79

Relation between relative growth factor and maximum daily temperature
in the "dry" treatments

equations. Characterization of the daily status of the substrate was something less than completely adequate. For example, at the lower levels of soil moisture depletion, matric suction at a given point in the rhizosphere may change appreciably over a 24-hour period. Further, the matric suction at different points in the rhizosphere at a given time may vary. Thus, selecting a single value for effective matric suction over a day's time becomes an approximation rather than an actuality. Deriving a single value for effective osmotic pressure of the solution at the surface of the absorbing roots where major water absorption was taking place during the course of a given day was even less satisfactory. At the time this study was undertaken, soil salinity sensors were not available for insertion into various parts of the rhizosphere of each culture. One must conclude that there is a real need for improved characterization of the effective water potential in a rhizosphere varying in moisture content and salinity level.

Although only a single plant was grown in each culture containing 200 pounds of soil, the soil mass was inadequate even though the experimental period occurred at a time of year when evapo-transpiration was at a minimum. The rate of change in soil moisture content per day was just too rapid in cultures with the larger plants for precise characterization.

These few comments on the inadequacies of the experimental set-up are offered with the thought that good judgement comes from experience, and experience comes from bad judgement.

SUMMARY

During December 1950 and January 1951, a single castor bean plant was grown in each of 12 oil drums, and each drum contained 200 pounds of Pachappa sandy loam. One-third of the cultures received no salinization, one-third received added Na Cl to the amount of 0.025 percent of the soil mass, and the other one-third received 0.05 percent Na Cl. Half of the cultures at each salt level were irrigated when soil moisture depletion was barely below field capacity, and the other half were not irrigated until soil moisture content approached the permanent wilting percentage.

Each culture was equipped with four manometric tensionmeters, and each culture was weighed each day to a precision of 0.1 pounds. Soil samples were taken periodically with a miniature soil tube to check soil moisture content at different horizons and salt content of the samples. Continuous records were maintained of solar radiation, aerial temperature, and relative humidity.

The length of the mid-rib on each leaf on each plant was measured in millimeters between 8 and 9 a. m. each day.

Daily water loss per culture was evaluated by multiple regression equations as related to environmental conditions and total leaf area of the respective plant. Total leaf area was far and away the dominant factor determining the magnitude of daily water loss per culture. In

salinized cultures, increasing osmotic pressure of the soil solution was associated with a decrease in water loss per sq. cm. of leaf surface per day. In the unsalinized "dry" cultures, increasing matric suction of the soil was related to a decrease in water loss per unit area of leaf surface. Increasing solar radiation had a quite consistent effect in increasing water loss per unit of leaf surface. For the most part, increased level of the maximum daily temperature was associated with increasing water loss per unit of leaf surface. Regression analysis indicated that the status of relative humidity had no effect on rate of water loss from the leaves.

Growth of the leaves as measured by elongation followed logistic trends that were invariably non-symmetrical. Daily deviations of actual leaf measurements from the values derived from the fitted curve were used in multiple regression analysis to evaluate environmental impact on leaf growth. This approach did not prove to be satisfactory. Richards' "m" factor was calculated for specified leaves towards the correcting of the non-symmetrical logistic growth curves to symmetry. This procedure produced a plethora of statistics, but it was not deemed satisfactory for the evaluation of environmental impact upon the variation in daily leaf growth increment.

Measurements of daily leaf length were converted to values expressing leaf area. Total leaf area per day was calculated for each plant. This enabled calculation of daily increments in total leaf area. Fisher's

"relative growth rate", $\frac{1}{A} \frac{dA}{dt}$, was determined for each day on each plant. Time, or biological age of the leaf, was found to be the main determinant in the magnitude of the values for relative growth rate. Thus, the latter values were adjusted for the effects of biological age, in a multiple regression analyses of the effects of environmental factors on growth rate. Calculated osmotic pressure of the soil solution was found to be the dominant environmental factor affecting relative growth rate.

A rationale was presented to suggest that the computer analyses did not adequately distinguish between the effects of matric suction and osmotic pressure because of the high degree of intercorrelation between these two factors. Also, inferences were presented to the effect that the calculated average osmotic pressure of the soil solution in a culture was not the effective osmotic pressure at the surface of the absorbing roots.

Following an arbitrary procedure, values for "adjusted" osmotic pressure were calculated for each culture for each day.

By using the non-salinized cultures, net regression curves for the effect of matric suction on relative growth rate were determined. In the "wet" cultures, the growth function increased with increase in matric suction from 0.08 to 0.3 bars, and then leveled off. The adverse effect of the lowest level of matric suction on the growth function was assumed to be associated with impaired soil aeration prevailing at matric suctions at or below 0.1 bars.

The regression coefficients for the effects of matric suction were then locked into multiple regression equations to ascertain the effects of adjusted osmotic pressure, solar radiation, and maximum daily temperature. Each factor was assigned coefficients to permit curvilinear relationship in the logarithmic form of the equations.

Increasing values for adjusted osmotic pressure consistently showed a highly significant negative effect on relative growth rate in all treatments.

Increased level of daily solar radiation tended to have a positive effect on the growth function. However, the relation was found to be definitely negative for the "high salt - wet" cultures.

Increased level of maximum daily temperature tended to have an adverse effect on the growth function. Plants on the "no salt - wet" cultures provided for the main exception.

A brief discussion is presented on the need for far better characterization of variation in the water potential over various portions of the rhizosphere in experiments such as the one examined.

LITERATURE CITED

1. Army, T. J., and Ostle, B. The association between free-water evaporation and evapotranspiration of spring wheat under the prevailing climatic conditions of the Plains Area of Montana. Proc. Soil Sci. Soc. Amer. 21: 419-472. 1957.
2. Bertalanffy, L. von. Quantitative laws in metabolism and growth. Quart. Rev. Biol. 32: 217-231. 1957.
3. Blaney, H. F. Monthly consumptive use of water by irrigated crops and natural vegetation. Int. Un. Geod. and Geoph. Int. Assoc. of Sci. Hydrol., Gen. Assem. Toronto. 2: 431-439. 1958.
4. Bower, C. A., and Wadleigh, C. H. Growth and cationic accumulation by four species of plants as influenced by various levels of exchangeable sodium. Soil Sci. Soc. Amer. 13: 218-223. 1948.
5. Eaton, F. M. Water uptake and root growth as influenced by inequality in the concentration of the substrate. Plant Physiol. 16: 545-564. 1941.
6. Eaton, F. M. The osmotic and vitalistic interpretation of exudation. Amer. Jour. Bot. 30: 663-673. 1943.
7. Ezekiel, M., and Fox, K. A. Methods of correlation and regression analysis. J. Wiley & Sons, N.Y. 1959.
8. Fisher, R. A. Some remarks on the methods formulated in a recent article on "The quantitative analysis of plant growth." Ann. Appl. Biol. 7: 367-372. 1921.
9. Gardner, W. R. Soil water relations in arid and semi-arid conditions. In Plant-Water Relationships in Arid and Semi-Arid Conditions. UNESCO Reviews of Research, pp. 37-61. 1960.

10. Gardner, W. R. Internal water status and plant response in relation to the external water regime. In Plant Response to Climatic Factors. UNESCO, Paris. pp. 221-226. 1973.
11. Gauch, H. G., and Wadleigh, C. H. Effects of high salt concentrations on growth of bean plants. Bot. Gaz. 105: 379-387. 1944.
12. Halstead, M. H., and Covey, W. Some meteorological aspects of evapotranspiration. Proc. Soil Sci. Soc. Amer. 21: 461-468. 1957.
13. Hayward, H. E., and Long, E. M. Anatomical and physiological responses of the tomato to varying concentrations of sodium chloride and sodium sulphate in nutrient solutions. Bot. Gaz. 102: 437-462. 1941.
14. Hayward, H. E., and Bernstein, L. Plant-growth relations on salt-affected soils. Bot. Rev. 24: 584-635. 1958.
15. Hoerl, A. E., Jr. Fitting curves to data. In Chemical Business Handbook. John H. Perry (Ed.), McGraw-Hill, N.Y. 1954.
16. Kramer, P. J. Plant and soil water relationships. McGraw-Hill, N.Y. 1969.
17. Laboratory Staff, U.S. Salinity Lab. Diagnosis and improvement of saline and alkali soils. Edited by L. A. Richards. Agric. Handbook No. 60. U.S.D.A. 1954.
18. Lemon, E. R., Gaser, A. H., and Satterwhite, L. E. Some aspects of the relationship of soil, plant, and meteorological factors on evapotranspiration. Proc. Soil Sci. Soc. Amer. 21: 464-468. 1957.

19. Long, E. M. The effect of salt additions to the substrate on intake of water and nutrients by roots of approach-grafted tomatoes. *Am. Jour. Botany* 30: 594-601. 1943.
20. McGuinness, J. L. A comparison of lysimeter-derived potential evapotranspiration with computed values. U.S.D.A. Tech. Bull. 1452. 1972.
21. Milthorpe, F. L. The income and loss of water in arid and semi-arid zones. In *Plant-Water Relationships in Arid and Semi-Arid Regions*. UNESCO. pp. 9-36. 1960.
22. Philip, J. R. The soil-plant-atmosphere continuum in the hydrological cycle. *Hydrological Forecasting*. Tech. Note No. 92. 1969.
23. Richards, F. J. A flexible growth function for empirical use. *Jour. Expt. Biol.* 10: 290-300. 1959.
24. Richards, F. J. The quantitative analysis of growth. In *Plant Physiology*. Vol. VA, edited by F. C. Steward. Academic Press, N.Y. 1969.
25. Richards, L. A., and Wadleigh, C. H. Soil water and plant growth. In *Soil Physical Conditions and Plant Growth*. Edited by B. T. Shaw, Academic Press, N.Y. 1952.
26. Richards, L. A., and Campbell, R. B. Use of thermistors for measuring the freezing point of solutions and soils. *Soil Sci.* 65: 429-436. 1948.
27. Richards, L. A. A soil salinity sensor of improved design. *Proc. Soil Sci. Soc. Amer.* 30: 333-337. 1966.
28. Slatyer, R. O. The effect of internal water status on plant growth, development and yield. In *Plant Response to Climatic Factors*. UNESCO, Paris. pp. 177-192. 1973.

29. Thornethwaite, C. W. An approach towards a rational classification of climate. *Geogr. Rev.* 38: 55-94. 1948.
30. Wadleigh, C. H. The integrated soil moisture stress upon a root system in a large container of saline soil. *Soil Sci.* 61: 225-238. 1946.
31. Wadleigh, C. H., and Bower, C. A. The influence of calcium ion activity in water cultures on the intake of cations by bean plants. *Plant Physiol.* 25: 1-12. 1950.
32. Wadleigh, C. H., and Ayers, A. D. Growth and biochemical composition of bean plants as conditioned by soil moisture tension and salt concentration. *Plant Physiol.* 20: 106-132. 1945.
33. Wadleigh, C. H., and Gauch, H. G. Rate of leaf elongation as affected by the intensity of the total soil moisture stress. *Plant Physiol.* 23: 485-495. 1948.
34. Wadleigh, C. H., Gauch, H. G., and Strong, D. G. Root penetration and moisture extraction in a saline soil by crop plants. *Soil Sci.* 63: 341-349. 1947.
35. Watson, D. J. The dependence of net assimilation rate on leaf-area index. *Ann. Bot. London.* 22: 37-54. 1958.

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