Recent studies (1, 7, 9) have indicated that an interrelationship exists between soil salinity and the soil moisture content in their effect on plant growth. These two factors may be logically evaluated in terms of the decrease in the specific free energy of the soil moisture. Thus, salinity may be expressed in terms of the osmotic pressure of the soil solution, and the soil moisture status with respect to surface force action is expressible in terms of the soil moisture tension in atmospheres. The sum of these two components has been termed the "total soil moisture stress" (7).

It is difficult to evaluate the moisture stress to which a plant is responding when grown on a given mass of saline soil. This moisture stress which is conditioning the entry of water into the roots will be largely affected by five variables: (a) the variation in salt distribution within the soil mass and its consequent effect on the variation in the osmotic pressure of the soil solution at a given moisture content; (b) variation in osmotic pressure in relation to change in moisture content; (c) variation in moisture tension in relation to moisture content; (d) variation in moisture content within the soil mass at a given time; and, (e) variation in total water content of the soil mass with time, i.e., over an irrigation interval. A method has been developed to integrate these variables as they obtain within a large container of saline soil (8). This method makes it possible to determine the relation of the theoretically uniform stress, S, throughout that part of the soil mass within which moisture movement into the plant is taking place, to the total moisture content, W, of the soil. That is,

\[ S = f(W) \]

This stress is called the integrated soil moisture stress.

Since the moisture content of the soil supporting a growing plant changes continuously with time, the integrated moisture stress in the soil also changes with time. If the curve is obtained which shows the integrated stress as a function of time, then the average integrated stress over a given time interval will be that constant stress represented by a horizontal line on the chart having under it the same area as that subtending the curve.

1 Contribution from the U. S. Regional Salinity and Rubidoux Laboratories, Riverside, California, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture, in cooperation with the eleven Western States and the Territory of Hawaii.

2 Principle Chemist, and formerly Associate Physiologist.
This average integrated stress is referred to as the average daily moisture stress, $S_a$. It may be formally expressed as

$$S_a = \frac{\int_{t_o}^{t_x} Sdt}{t_x - t_o}$$

where time, $t$, is expressed in days, and $t_o$ and $t_x$ are the limits of integration.

It has been observed with beans (7) and guayule (9) that there is a fairly close relationship between vegetative growth and the average moisture stress, if other factors affecting growth are not limiting and are kept as uniform as possible. Since the resultant growth response appears to be related to the average daily moisture stress, it should follow that daily variations in plant growth could be observed concomitant with the variations in moisture stress taking place over an irrigation cycle. It is the purpose of this report to present observations on this postulated relationship.

**Methods**

Cotton plants of the Acala P–18–C variety were grown individually in steel drums containing 100 pounds of adequately fertilized Fallbrook loam.

![Graph](https://www.plantphysiol.org)  
**Fig. 1.** The relation between moisture tension and moisture content together with variations in total moisture stress—tension plus osmotic pressure—when various amounts of salt, $Q$, have been added to the soil. In this case $Q$ is taken as the osmotic pressure of the soil solution when the soil contains 12% moisture.
This soil has a field capacity of 18% moisture and the wilting percentage is 6.1. The relationship between moisture tension and moisture content is shown in figure 1, as well as the variations in total moisture stress with moisture content when various amounts of salt have been added to this soil. The "control" plants were grown on this nonsaline soil with no added salt other than fertilizer. The "saline" plants were grown on soil to which 0.2% NaCl had been added. The saline cultures were alternately surface and sub-irrigated in order to maintain a more nearly uniform distribution of salt in the soil mass. After each irrigation, two cultures containing saline soils were discontinued and sampled with respect to salt distribution and moisture content. Soil salinity was evaluated in terms of the electrical conductivity of the extract from the saturated soil (5). The osmotic pressure of the soil solution at prevailing moisture contents was calculated by means of a previously ascertained relationship between these factors for this soil (1, 5). The drums of soil were weighed at 8 o'clock each morning. When the average moisture content of a given container of soil reached 12%, sufficient water was added to bring the average to 21%.
The length, L, of each leaf arising from the main axis of each plant was measured at the same time every morning during the course of this study. Thus, L was taken as a measure of plant size; and growth, G, may be defined for the present case as the rate of elongation of the leaves, or

\[ G = \frac{dL}{dt} \]

This paper is concerned with the relation of growth to moisture stress, or

\[ G = f(S) \]

Observations

Figure 2 presents the leaf-length data obtained from one of the control plants. The observations tend to follow smooth curves suggesting that the minor variations present were not related to the irrigation schedule. That is, it appears that the small fluctuations in moisture stress, from 1 to 3 atmospheres, within the control cultures were without observable effect on rate of leaf elongation.

The typical observations on leaf elongation for one of the plants on saline soil are shown in figure 3. It should be noted that growth of an expanding
leaf just about ceased by the time the soil was ready for an irrigation. If
the leaf was incompletely developed, elongation resumed at a fairly rapid
rate immediately following an irrigation and nearly ceased by the time of
the next irrigation.

The variation in the average moisture content with time is shown in fig-
ure 4. This is the same as the total water content in pounds, since the dry

weight of soil per container was 100 pounds. From the previously estab-
lished relation of stress to water content it is possible to calculate the stress
at each moisture content and thus represent the stress also as a function of
time in this figure, i.e.,

\[ S = f(t) \]

As pointed out elsewhere (9), the shape of these stress-time curves is spe-
cific for a given culture of soil during a given irrigation interval, in that they
depend on the status of salt distribution within the soil and the rate of water
removal from the soil.

The shapes of the leaf elongation curves within a given irrigation period
are essentially parabolic. Hence, a second degree equation may be fitted to
the data of such segments of these curves by the method of least squares so that leaf length, \( L \), may be expressed as an explicit function of time, \( t \), as follows:

\[
L = a + bt + ct^2
\]

where \( a \), \( b \), and \( c \) are constants. Hence, leaf growth which has been defined as \( \frac{dL}{dt} \) may be expressed by the relation

\[
\frac{dL}{dt} = b + 2ct.
\]

It was indicated above that within any given irrigation cycle, moisture stress can be empirically expressed as a function of time. It follows then that leaf length may be correspondingly derived as a tentative function of stress. Figure 5 presents the data for leaf length in figure 3 plotted against corresponding observations for moisture stress shown in figure 4. These relationships are also essentially parabolic and could be expressed as

\[
L = a' + b'S + c'S^2
\]

where \( a' \), \( b' \), and \( c' \) are constants determining the locus of a given curve.

Since leaf elongation tends to cease at the higher values of stress, it would be helpful to ascertain the intensity of stress associated with cessation of growth. This could be approximated by visual observation on figure 5, but personal bias would not be involved if this intensity of stress were arrived at mathematically from the empirical equation for the length of a given leaf as a function of stress during a given irrigation cycle.
As leaf elongation approaches cessation, the parabolic curve for the relation approaches a maximum. That is, the point at which the parabola passes through a maximum will be the theoretical point at which leaf elongation stops. It is to be recalled that the derivative of a parabolic equation becomes zero when the curve passes through a maximum. On differentiating, the previous equation becomes

$$\frac{dL}{dS} = b' + 2cS.$$  

When growth ceases, i.e., when $\frac{dL}{dt} = 0$, it follows that leaf length becomes invariant with respect to stress. Thus, at this time, $\frac{dL}{dS} = 0$. Consequently, the stress corresponding to the cessation of growth may be found from the relation

$$S = -\frac{b'}{2c'}.$$  

To illustrate the mathematical procedure, the figures involved in the reduction of a typical set of data are presented in table I.

**TABLE I**

Observations made on the fifth leaf of plant no. 1 during irrigation cycle A

<table>
<thead>
<tr>
<th>Time (t) after irrigation</th>
<th>Length of leaf (L)</th>
<th>Calculated from $L = f(t)$</th>
<th>Calculated from $L = f(S)$</th>
<th>Calculated from W</th>
<th>Calculated from $S = f(t)$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Days</strong></td>
<td><strong>Measured</strong> mm.</td>
<td><strong>Calculated</strong> mm.</td>
<td><strong>Calculated</strong> mm.</td>
<td><strong>atm.</strong></td>
<td><strong>atm.</strong></td>
</tr>
<tr>
<td>3</td>
<td>45</td>
<td>43.7</td>
<td>43.9</td>
<td>6.0</td>
<td>5.8</td>
</tr>
<tr>
<td>4</td>
<td>54</td>
<td>54.6</td>
<td>53.8</td>
<td>6.8</td>
<td>6.8</td>
</tr>
<tr>
<td>5</td>
<td>62</td>
<td>64.2</td>
<td>63.7</td>
<td>7.7</td>
<td>7.7</td>
</tr>
<tr>
<td>6</td>
<td>73</td>
<td>75.6</td>
<td>73.1</td>
<td>8.7</td>
<td>8.7</td>
</tr>
<tr>
<td>7</td>
<td>80</td>
<td>79.8</td>
<td>79.5</td>
<td>9.5</td>
<td>9.7</td>
</tr>
<tr>
<td>8</td>
<td>86</td>
<td>85.8</td>
<td>85.6</td>
<td>10.4</td>
<td>10.7</td>
</tr>
<tr>
<td>9</td>
<td>91</td>
<td>90.6</td>
<td>91.6</td>
<td>11.6</td>
<td>11.6</td>
</tr>
<tr>
<td>10</td>
<td>95</td>
<td>94.1</td>
<td>94.8</td>
<td>12.6</td>
<td>12.6</td>
</tr>
<tr>
<td>11</td>
<td>96</td>
<td>96.4</td>
<td>96.5</td>
<td>13.6</td>
<td>13.6</td>
</tr>
<tr>
<td>12</td>
<td>97</td>
<td>97.5</td>
<td>96.4</td>
<td>14.8</td>
<td>14.6</td>
</tr>
</tbody>
</table>

By the method of least squares, the empirical relation between $L$ and $t$ for these data was found to be:

$$L = 3.8 + 15.13 t - 0.610 t^2.$$  

Hence,

$$\frac{dL}{dt} = 15.13 - 1.22 t.$$  

When $\frac{dL}{dt} = 0$,

$$t = \frac{15.13}{1.22} = 12.4 \text{ days},$$

the calculated time at which leaf elongation stopped. The data in table I also gave the following empirical relation:

$$S = 2.86 + 0.975 t.$$  

Thus, when leaf growth theoretically ceased on the 12.4th day,

$$S = 2.86 + 0.975 \times 12.4 = 14.9 \text{ atmospheres.}$$
As indicated above, it is not necessary, mathematically, to evaluate both \( L \) and \( S \) as functions of \( t \) before developing the relation between leaf length and stress. It may be shown from the data in table I that

\[
L = -62.26 + 22.46S - 0.793 S^2
\]

and that

\[
\frac{dL}{dS} = 22.46 - 1.586 S.
\]

Hence, when \( \frac{dL}{dS} = 0, \)

\[
S = \frac{22.46}{1.586} = 14.2 \text{ atmospheres}
\]

at the time when leaf elongation theoretically stopped.

The calculated values for \( L \) as a function of \( t \) in table I are slightly different from those calculated from the equation for \( L \) as a function of \( S \). Of especial importance is the evidence that the derived curve, \( L = f(t) \), had not passed through its maximum as of the 12th day, whereas the derived curve, \( L = f(S) \), had passed through its maximum at this respective time. It is apparent that physiological logic dictates that growth be evaluated as a function of time, with the stress limiting to growth being calculated for the time when \( \frac{dL}{dt} = 0 \). Since the mathematical labor is considerably reduced by deriving \( L \) directly as a function of \( S \), the values reported herein were calculated by the latter method. The difference between the limiting stress values calculated by the two different methods is well within experimental error.

It should be noted that some of the leaf elongation curves in figures 4 and 5 are somewhat sigmoid. Therefore, in deriving the constants for a given parabolic equation it was advisable to eliminate those values below the inflection point of an apparent sigmoid relationship.

Figure 6 shows the rate of change of leaf length as related to stress, i.e.,

\[
\frac{dL}{dS} = b' + 2c'S.
\]

The maximum rate of change of leaf length with respect to stress occurs, theoretically, when the stress is zero and is equal to the constant \( b' \) in the equation. This value varied from 5.75 for the seventh leaf during irrigation cycle C to 24.6 for the seventh leaf during irrigation cycle B. However, it is apparent from the curves in figure 6 that for those leaves for which \( b' \) is large, the rate of decrease of \( \frac{dL}{dS} \) with respect to \( S \) is also large. Consequently, the regression lines intercept the abscissa for moisture stress within a narrow range of values. This is shown more fully in table II, which presents the growth-limiting values as calculated for all cases.

There are minor variations in the values of moisture stress limiting to growth among the leaves of a given plant. There are similar variations among observations for respective leaves on different plants. Nevertheless, it is indeed remarkable that these values average close to 15 atmospheres. When one takes into account the inherent errors in the method-
ology, it is surprising that variation of the individual observations around the mean were not greater.

It is pertinent to note that Richards and Weaver (4) state that the growth of most crop plants stops before the soil moisture tension reaches 15 atmospheres and the condition of permanent wilting is attained. They have shown that for most soils the fifteen-atmosphere percentage lies within the wilting range of soil moisture.

Furr and Taylor (3) made daily measurements on the size of lemon fruits as the soil under the tree progressively dried out. They used the apparent rate of increase in volume of the fruits as an index of turgescence within the tree. Their observations indicated that as the soil moisture is depleted a turgor deficit arises within the tree before the first visible sign of wilting appears. That is, growth was checked by water deficits within the plant, induced by increasing soil moisture stress. Thut and Loomis (6) reach this same conclusion from their studies involving consideration of many environmental factors in addition to supply of available soil moisture.

The data here presented are in substantiation of the theoretical considerations of Broyer (2) on the movement of water into plants. Of especial interest is his diagrammatic representation (see p. 20) showing the relationship between the various osmotic and hydrostatic forces and the relative

![Figure 6](https://example.com/fig6.png)

**Fig. 6.** The rate of change of leaf length as related to moisture stress.
volumes of the cells subject to these forces. Relative volume is shown to be related to the hydrostatic specific free energy of the internal phase, i.e., to turgor pressure. In an absorbing cell of the root, this hydrostatic specific free energy is equal to the sum of the influx specific free energies of the cells diminished by the specific free energy of the soil moisture. In other words, enlargement of plant tissues—growth—is a direct function of turgescence which in turn is partially conditioned upon the force with which water is withheld from the plant. It follows, therefore, that the observations on leaf elongation herein presented are in line with BROYER’s theoretical treatment of plant-water relations.

**TABLE II**

<table>
<thead>
<tr>
<th>IRRIGATION CYCLE</th>
<th>LEAF NO.</th>
<th>S = - b'/2e' when dG/dS = 0</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PLANT NO. 1</td>
<td>PLANT NO. 2</td>
</tr>
<tr>
<td>1st</td>
<td>atm.</td>
<td>atm.</td>
</tr>
<tr>
<td>Fourth</td>
<td>13.8</td>
<td>15.6</td>
</tr>
<tr>
<td>Fifth</td>
<td>14.2</td>
<td>15.9</td>
</tr>
<tr>
<td>Sixth</td>
<td>16.7</td>
<td>18.1</td>
</tr>
<tr>
<td>2nd</td>
<td>atm.</td>
<td>atm.</td>
</tr>
<tr>
<td>Fourth</td>
<td>13.0</td>
<td>14.1</td>
</tr>
<tr>
<td>Fifth</td>
<td>13.2</td>
<td>14.8</td>
</tr>
<tr>
<td>Sixth</td>
<td>14.1</td>
<td>16.7</td>
</tr>
<tr>
<td>Seventh</td>
<td>14.2</td>
<td>13.1</td>
</tr>
<tr>
<td>3rd</td>
<td>14.3</td>
<td>13.1</td>
</tr>
<tr>
<td>Seventh</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eighth</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>13.8</td>
<td>15.1</td>
</tr>
</tbody>
</table>

**Summary**

The rate of leaf elongation on cotton plants was ascertained with respect to increasing intensity of the soil moisture stress. Leaf elongation virtually ceased at the higher intensities of induced stress and resumed on alleviation of the stress by irrigation. During a given irrigation cycle, elongation was expressed empirically as a second degree function of soil moisture stress. This functional relationship was characterized by an approach to a maximum at the theoretical time at which growth ceased. Since the derivative becomes zero at a maximum, this value is used in solving the differentiated equations for the intensity of soil moisture stress limiting to leaf elongation by using the empirically derived constants for the functional relationship between leaf length and moisture stress. This procedure gave values consistently close to 15 atmospheres for the moisture stress inducing leaf-growth cessation for (a) different irrigation cycles during the growth of a given leaf; (b) different leaves on the same plant; and, (c) leaves on different plants.
LITERATURE CITED


