The Effect of Salt on the Growth of Salicornia.

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With Plate VIII and four Diagrams in the Text.

CERTAIN plants grow in soils that contain a considerable percentage of mineral salts. Sodium chloride is the most common of these salts and is the one most widely distributed. In this country the land impregnated with salt is only found near the coast in such a position that it is periodically covered by sea water. These areas are known as salt marshes and are covered by a very characteristic vegetation. The plants that form this vegetation have always aroused considerable interest, as their habit is obviously different from that of the typical mesophytic plant. The difference of appearance is due to the marked succulence of the majority of the species inhabiting the salt marshes. As early as 1876 Batalin[1] correlated this succulence with the presence of salt in the soil, as he found that 'salt plants' cultivated under ordinary conditions in the botanical gardens of St. Petersburg lost their usual characteristics, but if they were treated with solutions of sodium chloride they developed normally. At a later date Batalin[2] made cultivation experiments with plants of *Salicornia herbacea*, L., watering them with various salt solutions, and he found that the typical soft and fleshy habit was developed only when sodium chloride was present.

More recently the experiments of Lesage[3] have shown that ordinary non-succulent plants, e.g. *Lepidium sativum*, tend to become fleshy when cultivated in soil watered with solutions of sodium chloride. It is therefore probable that the presence of salt in the tissues of a plant has such an influence on the whole physiology of the plant as to alter its general structure, producing as one of the results the characteristic succulence seen in salt marsh plants.

The number of plants composing the vegetation of a salt marsh is

[1] Batalin, A.: Cultur der Salzpflanzen. Regel, Gartenflora, 28, 1876.

[2] Batalin, A.: Wirkung des Chlornatriums auf die Entwicklung von *Salicornia herbacea*, L. (Bull. du Congrès international de bot. et d'horticulture. St. Petersburg, 1886). Ref. in Bot. Centralbl. xxvii, 1886.

[3] Lesage, M. Pierre: Recherches expérimentales sur les modifications des feuilles chez les plantes maritimes. Revue générale botanique, t. ii, 1890.

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comparatively small, and of this number the various species of *Salicornia* and *Suaeda* occupy the most exposed positions, and may perhaps be regarded as among the most typical of the plants. They are very succulent and contain a considerable amount of sodium chloride in their tissues. It seems to follow from the culture experiments of Batalin that at least one of these plants, e.g. *Salicornia herbacea*, L., has become so specialized as to require sodium chloride for its normal development, though it can grow in ordinary soils when freed from the competition of other plants.

The effect of salt on the growth of plants is somewhat uncertain. Lesage[1] found that the height of plants of *Lepidium sativum* decreased with the increase of sodium chloride in the soil, while Stange[2] found that plants treated with certain salt solutions, e.g. of potassium nitrate, also decreased in height. With regard to the salt marsh plants themselves, Ganong,[3] describing the plants found on the Bay of Fundy marshes, says of *Salicornia herbacea*, L., that the plants varied 'in size inversely with the saltness of the habitat'. It was in the endeavour to obtain more information of the effect of sodium chloride that, some years ago at the suggestion of Professor F. W. Oliver, I made some experiments on the growth of these plants. I would like here to thank Professor Oliver for suggesting this work to me, and also for his kindness in bringing the seedling plants from the Bouche d'Erquy and for taking the photograph from which Pl. VIII was made.

The experiments were made with *Salicornia* and *Suaeda* seedlings, which were cultivated in the presence of various amounts of sodium chloride. In this way the effect of different amounts of salt on the growth of the plants was ascertained.

The experiments were of two kinds and may be considered under the two following divisions:

I. Seedlings cultivated on their natural soil, and treated with solutions containing various percentages of Tidman's sea salt.

II. Seedlings cultivated in nutritive solutions to which definite quantities of sodium chloride had been added.

I.

Pieces of turf were brought from the Bouche d'Erquy in Brittany. The turf was composed chiefly of seedlings of *Salicornia ramosissima* or *Suaeda maritima* and of *Glyceria maritima*. The turf had been obtained from different parts of the marsh, so that some pieces bore *Salicornia* seedlings and *Glyceria*, while others had *Suaeda* seedlings and *Glyceria*. Sods were cut from the turf so that they just fitted into shallow porous earthenware

[1] Lesage, loc. cit.

[2] Stange, B.: Beziehungen zwischen Substratconcentration, Turgor und Wachsthum bei einigen phanerogamen Pflanzen. Bot. Zeit., 50, 1892, p. 349.

[3] Ganong, W. F.: Vegetation of the Bay of Fundy Marshes. Bot. Gaz., vol. xxxv, 1903, p. 357.

pans. The pans were divided into four sets of six, two (A and B) with seedlings of *Salicornia ramosissima*, and two (C and D) with seedlings of *Suaeda maritima*. In each lot each pan was treated differently, and was watered with a solution containing one of the following quantities of Tidman's sea salt, 0%, 1%, 2%, 3%, 4%, or 5%. Solutions of Tidman's sea salt were used so that the plants should be exposed to an influence resembling, as far as possible, that of sea water.

The sods were cut near the end of April when the seedlings were very young. These were apparently all at the same stage of development, their cotyledons were expanded, but no epicotyls were visible above the level of the cotyledons. The experiments were begun on April 28 and were continued till June 25. The plants were exposed to the different degrees of salinity by immersing the pans in the various solutions for a period of two hours or longer every seven days or so. If the soil became dry between the immersions, the pans were watered with equal volumes of the appropriate solutions.

It was soon evident that the rate of growth of *Salicornia* and *Suaeda* differed in the various pans, and this difference became increasingly evident as the treatment was continued. Certain plants, five in number, were chosen in each pan, and the rate of growth of their epicotyls noted by measurements taken at intervals. But, as there was found to be considerable variation in the height of the plants in the same pan, the curves of growth so obtained are not of sufficient value to warrant their reproduction here. The sods were untouched before the treatment began, the seedlings were allowed to remain as the seeds had fallen and germinated, so that they were not at all evenly distributed. It was thought therefore that the variation in the height of the individual plants in the same pan was due to the competition of the plants with one another, and with the *Glyceria* which was also present. In spite of this variation in size of some of the plants, the effect of the various degrees of salinity on the growth of the plants as a whole was very evident, and is best shown by a comparison of the average height obtained by the plants in the different pans. On June 1, nearly five weeks after the treatment was begun, the length of the epicotyl of each plant was measured and the average for each pan calculated. The figures obtained are given in the table below:

TABLE I.

Average height of plants in millimetres.

Tidman's sea salt.	*Salicornia ramosissima.*		*Suaeda maritima.*	
%	A	B	C	D
0	8·2	9·7	11·7	10·8
1	11·9	12·7	12·4	9·9
2	5·5	7·3	10·0	8·0
3	4·4	3·7	8·0	6·2
4	2·3	3·0	4·1	2·3
5	2·3	3·2	4·7	2·6

These results are represented graphically in Diagram 1, where the variation in height is plotted against the variation in salinity.

This diagram shows clearly that plants of *Salicornia* flourished best in the presence of a certain amount of salt, though growth was retarded if the

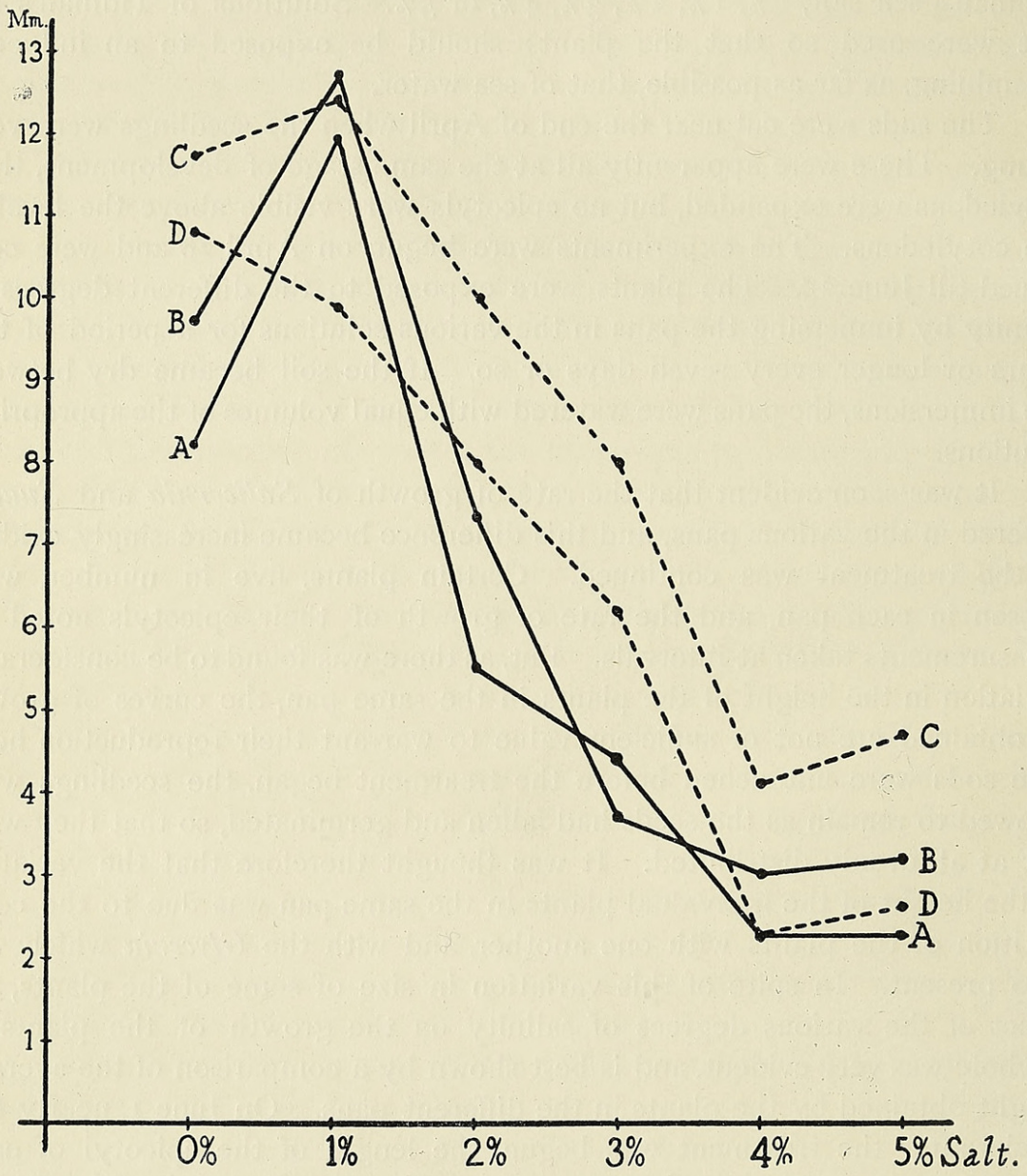


DIAGRAM 1.
Effect of degree of salinity on growth of *Salicornia* and *Suaeda*.
——— *Salicornia ramosissima*, pans A and B.
- - - - - *Suaeda maritima*, pans C and D.

amount of salt present increased beyond a certain limit. In these experiments the greatest growth took place in the pans treated with the 1% solution of Tidman's sea salt. The effect of salt on the growth of *Suaeda maritima* is not so clearly shown, as in one case it slightly increased the growth and in the other slightly decreased it. The plants were measured again on June 16, when the same variation in growth was found. A number

of the Salicornias in the pans treated with the 1 % solution of Tidman's sea salt and with distilled water were measured again on June 25, when it was found that the difference of growth was maintained. The average height of the plants was 39·2 mm. in the first case, while it was 29·9 mm. in the second.

The effect of salt on the growth of *Glyceria maritima* was also noted. In the pans treated with the higher percentages of salt, 3 %, 4 %, and 5 %, it was found that after a time the plants turned yellow and finally died, while growth was greatest in the pans treated with water containing no salt. On June 25 the average height of the grass in each pan was obtained, and the decrease in growth according to the increase in salinity is shown in Diagram 2. Here the dotted lines represent the height of the *Glyceria* in the four sets of pans, A, B, C, and D, while the unbroken line gives the average height of the *Glyceria*.

It seemed to follow from these experiments that *Salicornia ramosissima* grew best when it was treated with a somewhat dilute solution of Tidman's sea salt (1 %), a considerably weaker solution than that of sea water. The other two salt marsh plants experimented with were less tolerant of salt. *Suaeda maritima* grew as well without salt as with it, while *Glyceria maritima* flourished much better in its absence. The fact that the plants were grown in soil made it somewhat difficult to be certain what was the actual salinity of the water available for the plant. When the experiments were begun, as the pans were comparatively small, it was thought that by immersing them for some time in the various solutions the excess of salt in the soil would be washed out, and that the salinity of the water in the soil would be approximately the same as that of the solution in which the pans were immersed. It was obvious that there was a certain variability in this salinity as, between the periods of immersion, water was lost from the soil by evaporation and through the transpiration of the plants. In order to ascertain the amount of this variation estimations were made of the salinity of the soil water in certain of the sods before and after immersion. The salinity was obtained by estimating the amount of water in the soil and the amount of chloride present, and then calculating the amount of salt in 100 c.c. of water, the chlorides being calculated as sodium chloride. Portions of soil were taken from one set of pans on June 5, just before the pans were immersed in the various solutions. The period of immersion lasted two hours and a half, then the pans were allowed to drain ; a second lot of samples was taken on the morning of June 6.

The results of these analyses brought out the fact that not only was there a considerable variation in the salinity of the water of the soil in each pan, but also that this salinity was much greater than that of the solutions with which they were watered. It was found that the excess of salt was not washed out during the periods of immersion, but accumulated in the

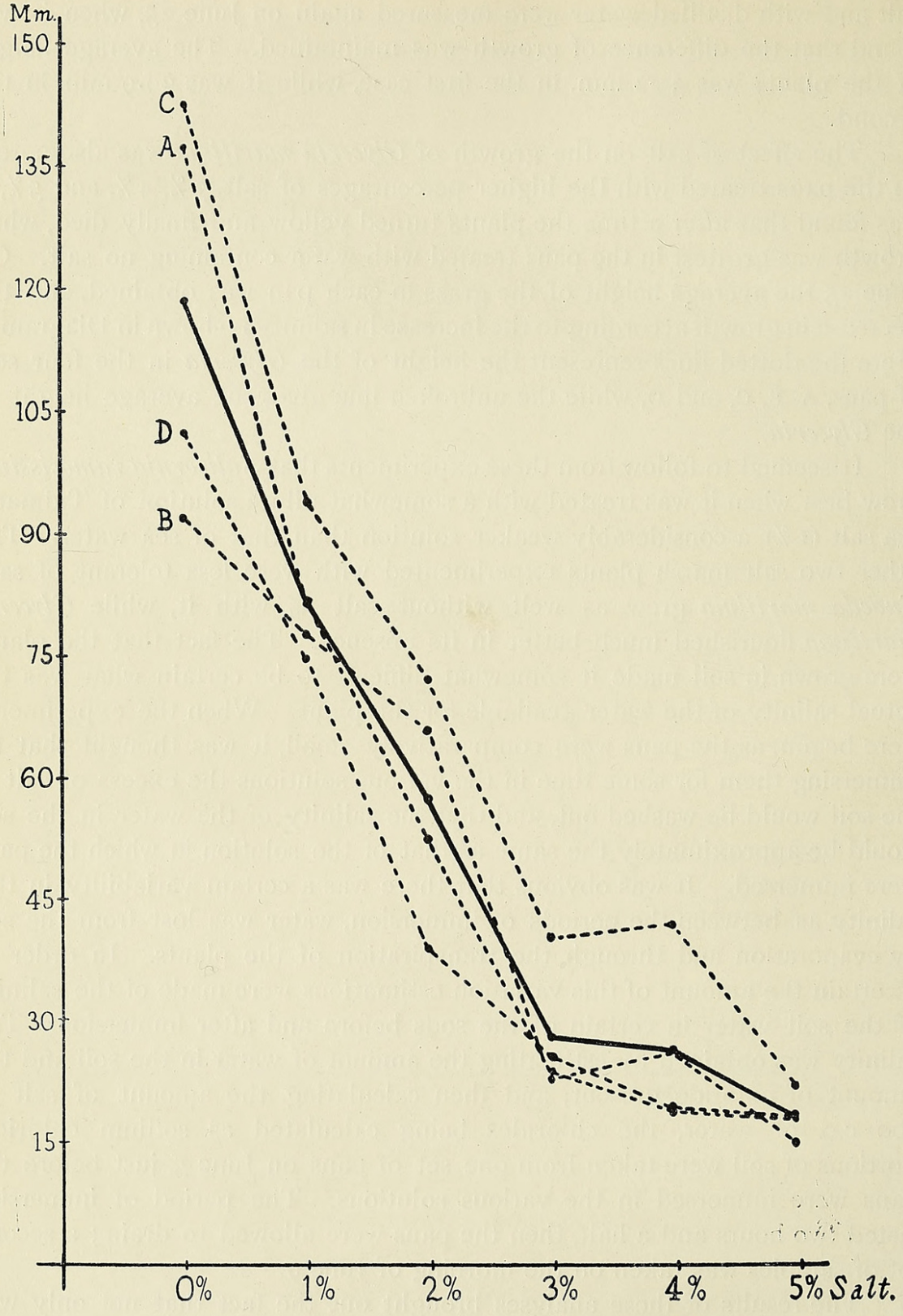


DIAGRAM 2.

Influence of salt on growth of *Glyceria maritima*.

- - - - Average height of plants in pans A, B, C, and D.

——— Average height of all plants.

soil so that the salinity of the water available for the plants in the different pans was much greater than was supposed. The results obtained are tabulated in Table II, and the figures give some idea of the range of salinity in the various pans:

TABLE II.

Range of salinity of water in soil.

Strength of solution of Tidman's sea salt.	*Salinity of water in soil.* *June 5 before immersion.*	*June 6 after immersion.*
%	%	%
0	1·4	0·6
1	5·6	2·5
2	9·9	5·7
3	17·8	10·5
4	18·8	12·1
5	15·0	11·2

It is evident from these figures that the pans watered with the 1 % solution, in which the greatest growth of *Salicornia* took place, contained soil the salinity of which varied within rather wide limits; in the sample analysed the variation was from 2·5 % to 5·6 %.

These experiments with plants grown in soil, while they show that plants of *Salicornia ramosissima* grow best in the presence of salt, do not show what percentage of salt is the most favourable, whether it is that which prevails in the normal habitat of the plants—approximately that of sea water—or not. The following year a series of water cultures was started to ascertain the effect of various amounts of sodium chloride on the growth of these plants.

II.

Various attempts were made to cultivate plants from seed brought from the salt marsh, but these were all unsuccessful; the seeds germinated, but the majority of the seedlings died before they had attained any size. Successful cultures were made with young seedlings brought from the Bouche d'Erquy. Three sets of cultures were started with the following plants: (1) *Salicornia oliveri*, (2) *Salicornia ramosissima*, and (3) *Suaeda maritima*. The plants were grown in glass jars containing nutritive solution, made up according to Sach's formula, with the addition of various amounts of sodium chloride. Six variations in the amount of sodium chloride were used, the solutions in the jars containing respectively 0 %, 1 %, 2 %, 3 %, 4 %, and 5 % of this salt. Care was taken that all other conditions for growth should be as far as possible equal for all the plants. It was hoped in this way to observe the effect of the different concentrations of sodium chloride on the growth of these three plants.

The cultures were started when the seedlings were quite young, their cotyledons were expanded, but no epicotyls were visible. Seedlings were

chosen as far as possible of the same size, and six were placed in each culture jar. The experiments were begun about the end of April.

The growth of the plants in the various solutions was compared by measurements of the lengths of the epicotyls. These measurements were begun on May 8 and were continued till the beginning of July. Here, as in the previous experiments, the results obtained for *Salicornia* differed from those obtained for *Suaeda*. It was found that the increase in length of the plants of *Suaeda* was approximately equal in the nutritive solution without the addition of sodium chloride and in that to which 1 % of this salt had been added, the total growth per plant in the first case being 112 mm. and in the second 110·2 mm. In the other jars the growth of the plants diminished as the amount of salt increased.

Plants of the two species of *Salicornia* grew much better in the presence of sodium chloride than in its absence. *Salicornia ramosissima* grew to approximately the same height in the jars with 2 % and 3 % of sodium chloride, and grew better in these than in the higher concentrations, while *Salicornia oliveri* grew rather more quickly in the solution containing 2 % of sodium chloride than in the other solutions.

The cultures were on the whole more successful with *Salicornia oliveri* than with *S. ramosissima*, probably because the seedlings of the former were more easily transferred without injury to the culture solutions, as the seeds had germinated naturally in sand. The results obtained with *S. oliveri* are therefore selected to be given in detail.

Table III gives the average increase in height of the plants of *S. oliveri* and shows how this was affected by the variation of the salinity. These averages were calculated from the measurements taken of the lengths of the main axis of the epicotyls of the six plants grown in each jar.

TABLE III.

Salicornia oliveri, Moss.

Date.	*Growth in mm., in different concentrations of* NaCl.					
	0 %	1 %	2 %	3 %	4 %	5 %
May 8	2·4	3·3	3·0	2·9	1·6	0·9
,, 15	3·3	4·9	5·4	3·8	2·1	0·6
,, 22	1·9	3·4	3·5	3·6	2·3	0·6
,, 29	1·5	4·7	5·3	4·7	2·8	1·0
June 5	1·1	4·0	5·6	4·4	3·3	2·1
,, 12	0·7	3·4	5·7	4·6	3·2	1·6
,, 20	0·5	3·4	4·9	4·4	3·7	1·6
,, 27	1·5	3·9	5·5	5·0	4·3	2·6
July 3	0·3	3·4	4·7	3·9	3·3	2·0
Growth in length by July 3	13·2	34·4	43·6	37·3	26·6	13·0

These dates and figures are plotted in Diagram 3, and give a series of growth curves for the different degrees of salinity. From these curves it can be seen that from the beginning of the experiment growth was greatest

when sodium chloride was present, and that the greatest growth took place when plants were grown in the solution containing 2% of sodium chloride. The curves also show that increase of salinity beyond a certain concentration is unfavourable to growth, it being slowest in the solution containing 5% of sodium chloride.

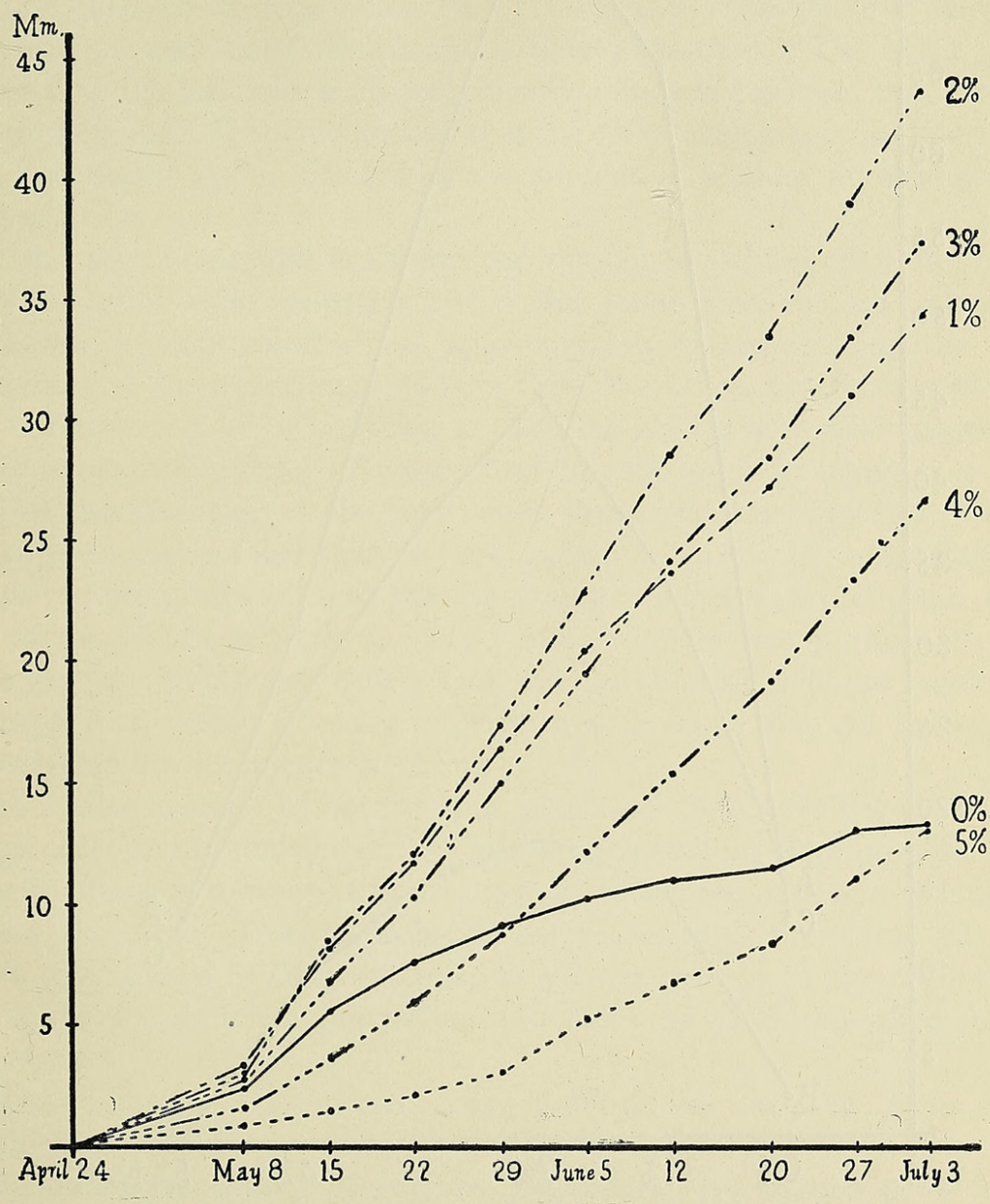


DIAGRAM 3.

Growth of *Salicornia oliveri*, Moss., in nutritive solutions containing various percentages of sodium chloride.

——————— 0% NaCl. —·—·— 1% NaCl. —··—··— 2% NaCl.
—···—···— 3% NaCl. —····—···· 4% NaCl. - - - - - 5% NaCl.

Many of these plants of *S. oliveri* branched; when this was the case the branches were also measured. It was found that the growth of the branches corresponded to the growth of the main axis, that is, that less growth took place in the absence of sodium chloride than when it was

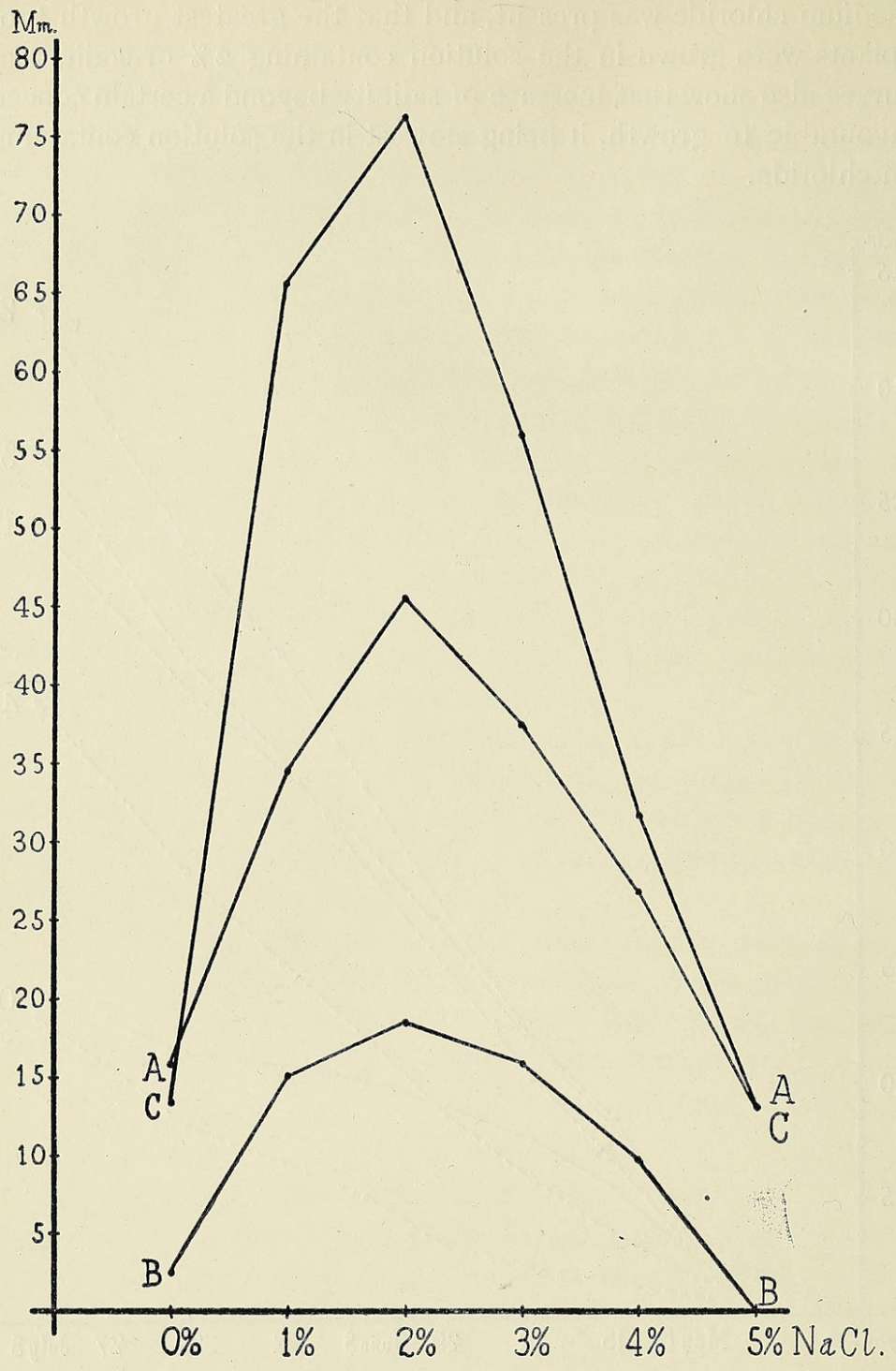


DIAGRAM 4.
Effect of NaCl on growth of *Salicornia oliveri*, Moss.
A. Average height of plants on July 3.
B. Average length of branches.
C. Average total growth per plant.

present in moderate quantity, and most when the solution contained 2% of this salt.

The measurements were discontinued on July 3, and the effect of the various degrees of salinity on growth till that date are shown graphically in

Diagram 4. This diagram gives three curves, A representing the average height which the main axes of the plants attained in the different solutions, B representing the average length of all the branches produced by the plants, and C the average total growth in length per plant (main axis and branches) under the various conditions of salinity.

The photograph from which Pl. VIII was made was taken at an earlier date, June 10, and shows the plants as they were then. The black paper surrounding the jars had been temporarily removed to show the development of the roots. It will be noticed that the root development is abnormally great, and that it also is affected by the amount of sodium chloride present in the solution.

After the photograph was taken the amount of sodium chloride present in each solution was estimated, and it was found that the amount of the salt present in each solution was approximately the same as at the commencement of the experiment, though the 2% solution had become slightly more concentrated. The jars were at this time refilled with fresh solutions.

It is perhaps worthy of record that the few measurements that were made of the diameter of the internodes show that this was less in those plants grown without salt than in those grown with it. In those plants of *S. ramosissima* grown without salt the average diameter of the lowest internode of the plants on June 20 was 2·7 mm., while it was 3·5 mm. in those plants grown with 2% and with 3% of sodium chloride. These results are in accord with those of former experiments, showing that the presence of salt increases the succulence of plants.

It is also worthy of record that plants of *S. oliveri* grown without sodium chloride did not flower, while those with sodium chloride did. Two plants in the 3% solution, three in the 4% solution, and one in the 5% solution flowered. This is probably the reason that the curve of total growth of *S. oliveri* in Diagram 4 shows greater growth in the 1% solution than in the 3%, as fewer vegetative branches were produced when flowers were formed.

The following conclusions may, I think, be deduced from these experiments:

1. *Salicornia oliveri*, Moss., and *Salicornia ramosissima* grow better in the presence of sodium chloride than they do in its absence, the greatest growth being when 2% to 3% of this salt is present. Higher percentages decrease the growth of the plants.

2. The effect of sodium chloride on the growth of *Suaeda maritima* is not so marked. Plants grow equally well in its absence as when a small quantity (1%) is present. Growth decreased when a greater amount of salt is present, and decreases with the increase in amount.

3. *Salicornia ramosissima* and *Suaeda maritima* can resist the presence of a large amount of sodium chloride, as is seen from the 'pan' experiments

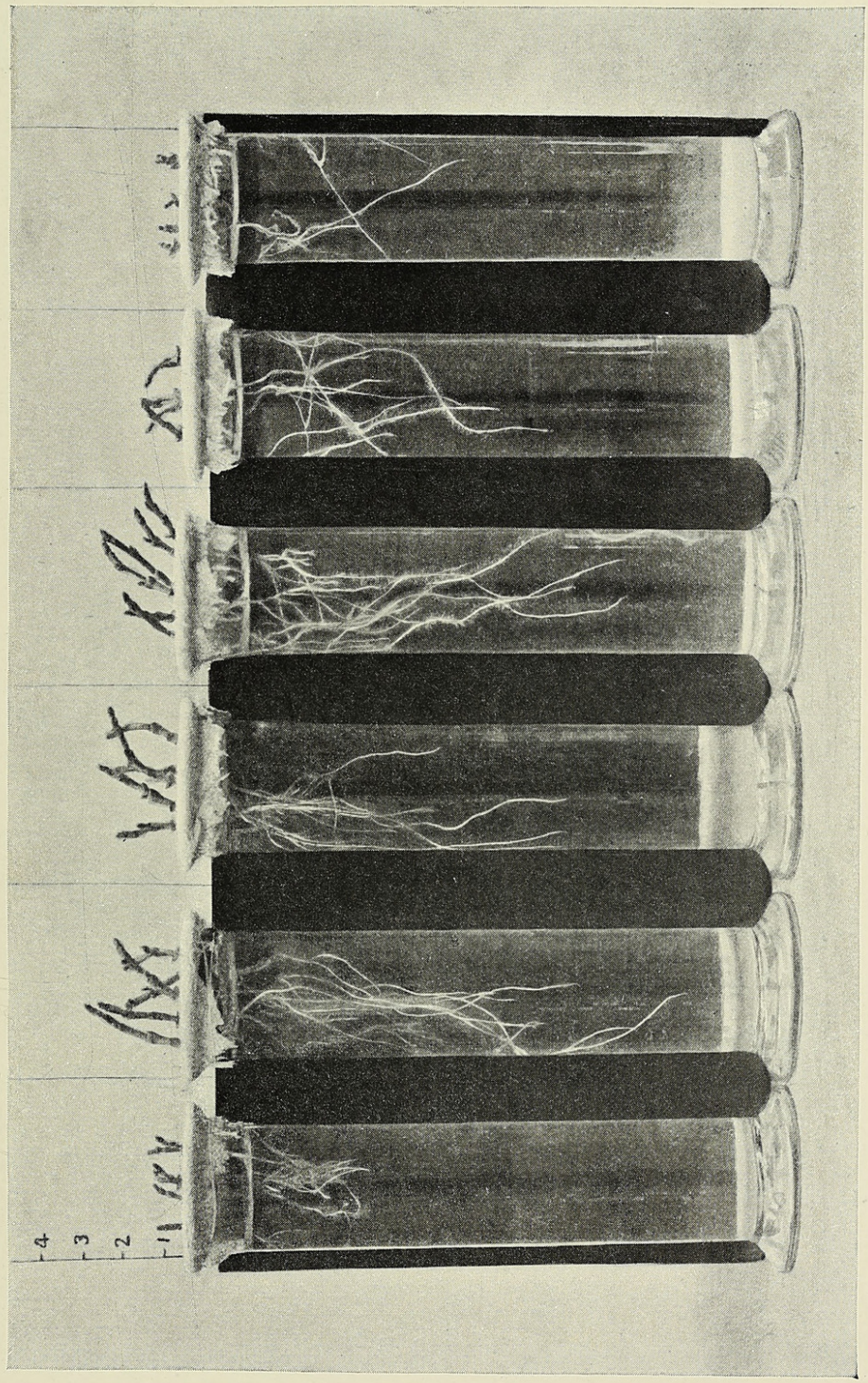
when the plants remained alive and green when the salinity of water in soil rose at times to 17 %, though they were not able to grow.

4. The growth of *Glyceria maritima* is decreased with the increase of the salinity of the soil.

After these experiments had been made, my attention was drawn to a paper by Mr. J. A. Terras,[1] in which he records the results he obtained with experimental cultures of certain salt marsh plants. He grew plants of *Salicornia herbacea*, *Suaeda maritima*, *Glaux maritima*, *Plantago maritima*, and *Spergularia media* in sand in pots suspended in vessels containing nutritive solutions (Knop's) made up with varying proportions of filtered and sterilized sea water. He continued his experiments for the much longer period of six months, from April to September. The general results recorded are similar to those given above. The effect of the salt varied with the different plants. *Salicornia*, *Suaeda*, and *Glaux* grew best when sodium chloride was present, while the greatest growth of *Plantago* and *Spergularia* took place in the absence of this salt.

When the amount of growth in the varying concentrations of solution is compared, it is seen to be greatest in the case of *Salicornia* and *Suaeda* in those pots suspended in solutions containing 0·92 % of sodium chloride; and the growth is found to decrease with increase in concentration of the solution. A difference is also seen on comparing the results of the higher percentages of salt, for plants of *Salicornia herbacea* and *Suaeda maritima* died in those pots in the liquid containing 3·2 % of sodium chloride, while in the experiments described above these plants were able to grow in much greater percentages of salt.

[1] Terras, J. A.: Notes on the Salinity of the Cell-sap of Halophytes with Relation to that of the Soil Solution in which they grow. Proc. Scot. Micro. Soc., vol. ix, nos. ii and iii.



Series of water cultures of *Salicornia oliveri*, showing effect of various strengths of sodium chloride on growth.