TOXICITY AND ACCUMULATION OF CHLORIDE AND SULFATE SALTS IN PLANTS[1]

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INTRODUCTION

The subject of salt toxicity, or "alkali," has been the object of experimental attention almost since the beginning of irrigation developments in the Western States. Recent advances in an understanding of the role of trace elements in plant growth and in the development of methods of physiological research have not only pointed to the need and provided the means for new studies of salt toxicity but they have also afforded an insight into some of the difficulties encountered by early investigators. Although salt toxicity and the quality of irrigation waters constitute but one aspect of the problem of profitable and permanent agriculture under irrigation, it is none the less a significant one, since decisions on the suitability of water supplies, the quantities of water required for soil leaching, and the financial advantages of drainage works and their capacities can be based intelligently only upon quantitative information on salt toxicity to plants. The wise selection of crops for saline soils must likewise rest on a knowledge of the relative tolerances of species and varieties of plants to the salt constituents of soil solutions.

When the present work was undertaken in 1934, there was a widespread belief in the western irrigated areas that if the neutral salts were below substantial concentrations the plants would be uninjured whereas if salts were above these concentrations injury would be pronounced. It appeared to the author, on the basis of evidence drawn from the literature as well as from observations in the field and in minor experiments, that there were weaknesses in this high-tolerance point of view and that additional investigations were needed. The experiments as originally undertaken had as a principal objective a study of the comparative reactions to chloride and sulfate salts of a number of crop plants grown together in a series of outdoor sand cultures differentially supplied with salts added to a base nutrient solution. Particular attention was paid to the development of plant symptoms that might be of diagnostic value under field conditions. The concentrations of salt constituents in the expressed sap of the plants were measured as a means of correlating injury with salt

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accumulation. Following the outdoor experiment, a number of greenhouse experiments were conducted for the purpose of obtaining a clearer idea of the character of the salt-injury curves through a series of low as well as intermediate and high concentrations of chloride and sulfate. The results of the first-mentioned work have been briefly referred to in an earlier paper (*10*).[4]

The literature bearing on the toxicity of chloride and sulfate salts, though not particularly extensive, is difficult to coordinate and summarize. The experimental procedures employed both in the field and in the laboratory have been diverse, and there is wide variability in the tolerance of different plants to chloride and sulfate ions. Moreover, the reactions of plants are in some measure dependent upon whether the chloride and sulfate are present as calcium, magnesium, or sodium salts, and upon climatic conditions as well. There has been no extensive work on this problem in recent years, and it has seemed better to refer in the text to results directly related to the present data rather than to undertake a general review of the literature

EFFECT OF CHLORIDE AND SULFATE SALTS ON A SERIES OF CROP PLANTS IN OUTDOOR SAND CULTURES (EXPERIMENT 1)

CLIMATIC CONDITIONS

The summer temperatures at Riverside, Calif., which is 40 miles inland from the Pacific Ocean, are not so high (table 1) as these prevailing in many of the interior valleys of the Southwest., nor are they as low as those of the coastal area. The climate at Riverside, usually tempered by the prevailing westerly winds from the Pacific, is occasionally hot and dry as a consequence of north and easterly winds coming off the Mojave and Colorado Deserts. The noonday relative humidity customarily falls in the 30-to-50 percent range, and the nights are almost always cool.

METHODS AND MATERIALS

The six sand beds used in this experiment have previously been described (9). The eight crops grown in short parallel rows in each

TABLE 1.-Climatological *data* [1] for *the period of the outdoor sand-culture experiment at Riverside, Calif., in 1934*

Month	Temperature						Relative humidity at 12 noon		
	Maximum			Minimum					
	Lowest	Highest	Mean of month	Lowest	Highest	Mean of month	Lowest	Highest	Mean of month
	° *F.*	° *F.*	° F.	° *F.*	° *F.*	° F.	*Percent*	*Percent*	*Percent*
May	74	107	88. 2	41	59	50. 2	10	48	31. 1
June	68	97	82	46	63	53. 7	22	68	46. 1
July	88	117	Y5.9	51	68	58. 7	14	51	33. 6
August	90	102	96. 1	52	64	57.4	15	46	32. 4
September	61	104	92. 8	41	63	55. 2	15	76	32
October	65	104	86	44	60	50	18	84	37. 6
November	61	93	74	34	52	44	15	94	43. 6

[1] Measurements made at Riverside by the University of California

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[4] Italic numbers in parentheses refer to Literature Cited, p. 397.

of the beds were, in order of planting from the north end to the south end, as follows: Dwarf milo (Sorghum vulgare Pers.), Acala cotton *(Gossypium hirsutum* L.), rooted lemon cuttings *(Citrus* limonia Osbeck), barley *(Hordeum vulgare* L.), navy beans *(Phaseolus vulgaris L.),* sugar beets *(Beta vulgaris* L.), alfalfa (Medicago *sativa* L.) (three cuttings), and tomatoes *(Lycopersicon esculentum* Mill.). All but the lemons were carried to maturity.

The treatments consisted of a control bed supplied with a base nutrient solution, which was the same in all the cultures, two chloride beds, one with 50 and one with 150 milliequivalents of chloride ion per liter, and three sulfate beds in which concentrations of 50, 150, and 250 milliequivalents, respectively, of sulfate ion per liter were maintained. Fifty percent of the chloride and sulfate ions was added as sodium salts, with the remaining *50* percent divided between calcium and magnesium salts. Equal proportions of the latter were used in the two chloride beds and also in the 50-sulfate bed, but because of the limitations of calcium sulfate solubility, magnesium sulfate was substituted for calcium sulfate above 20 milliequivalents per liter in the 150- and 250-sulfate beds. Tap water was used in the preparation and replenishment of the culture solutions.

The culture of a series of crop varieties together in sand beds or water cultures for a study of comparative physiology affords the best possible assurance that all are subjected to the same substrate conditions, including such factors as the concentrations of nutrient and toxic elements, temperatures in the root zone, oxygen, carbon dioxide, and water supply. Free exposure out of doors likewise tends to provide nearly the same gross climatic complex for all members of a planting. Nevertheless inequalities in exposure are created by reason of the differential responses of the several crops grown in each of the sand beds to superimposed variables, in this case the chloride and sulfate salts. Since plants are reduced in size by these salts, their exposure to light and wind is increased in relation to the control plants. This condition exist's also in field plantings.

The average composition of the tap water and the concentration of the constituents added in the preparation of the nutrient solutions are shown in table 2. The tap water contained 0.15 part per million of boron, and 0.85 p. p. m. was added in the preparation of each of the new solutions; 0.5 p. p. m. of manganese was also added. Iron was added daily as 10 ml. of a 5-percent iron tartrate solution. Zinc was not added directly, but measurements made on solutions of a

TABLE *2.-Composition of tap water and concentrations of salt constituents added to tap water in preparation of nutrient solutions*

Item	Constituent (milliequivalents per liter)								
	Ca	Mg	Na	K	HCO_3	SO_4	Cl	NO_3	H_2PO_4
Tap water	1.84	0.56	1.63	0.17	2.90	0.61	0.63	0.05	---- --
Constituents added:									
Control	6.00	2.0	--------	8	--------	2	--------	13	1
50-chloride	18.5	14.5	25	8	--------	2	50	13	1
150-chloride	43.5	39.5	75	8	--------	2	150	13	1
50-sulfate	18.5	14.5	25	8	--------	52	--------	13	1
150-sulfate	26.0	57.0	75	8	--------	152	--------	13	1
250-sulfate	26.0	107.0	125	8	--------	252	--------	13	1

subsequent experiment indicated that sufficient quantities were derived from the tap water and from impurities in the salts used in making up the solutions.

The eight crops were planted in parallel 18-inch rows in each of the six sand beds on April 17, 1934. These plantings were carried beyond germination with the base nutrient solution plus one-fifth of the final quantity of the chloride and sulfate salts. Additional fifths of salt were added on April 30 and May 2, 4, and 6. A half portion of each of the solutions with the final concentration of salt was then made up, used to flush the sand, and discarded. On the following dates new solutions were substituted for those in use: May 12 and 30, June 13 and 28, July 12, August 2 and 24, September 6, and October 5. The nitrate concentrations in all solutions were measured periodically, and deficiencies from the initial concentrations were replaced by additions of potassium nitrate or ammonium nitrate on July 19, July 26, August 16, and September 20.

The 180 liters of solution applied to the surface of the sand at each flooding of the beds was sufficient to replace by about one and a quarter times the solution held against gravity by the sand. The culture solutions returning to the lower reservoir were brought to volume with tap water after each use and then drawn up by suction into the upper reservoir to be used again. The solution held by the sand was replaced once each morning while the plantings were small, but as they became larger the operation was repeated a second time shortly after noon.

TOLERANCE

The relative tolerances of the series of crops to chloride and sulfate salts, as observed under the conditions of this experiment, are reported in table 3.

Table *3.-Growth and yield* [1] *of plants* in *experiment 1*

LEMONS, ROOTED EUREKA CUTTINGS (APR. 17-NOV. 19)

Nutrient solution	Plants surviving	Leaves retained		Total (leaves, stems, and roots)	
		Dry weight	Relative dry weight	Dry weight	Relative dry weight
	Number	Grams	*Percent*	Grams	Percent
Control	3	26	100	46	100
50-chloride	3	7	27	13	28
150-chloride	0	0			
50-sulfate	3	21	81	39	85
150-sulfate	3	8.7	32	15.2	33
250-sulfate	2	2.6	10	7.1	15

BEANS, NAVY (APR. 17-JULY 13)

Nutrient solution	Plants surviving	Seed		Entire plants	
		Dry weight	Relative dry weight	Dry weight	Relative dry weight
	Number	*Grams*	*Percent*	*Grams*	*Percent*
Control	5	347	100	671	100
50-chloride	5	135	39	271	40
150-chloride	0				
50-sulfate	5	225	65	443	66
150-sulfate	5	89	25	160	24
250-sulfate	0	0			

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[1] Sums of weights of plants in 18-inch rows are represented, unless otherwise indicated.

TABLE 3.—*Growth and yield of plants in experiment 1*—Continued

MILO, DWARF (APR. 17–SEPT. 19)

Nutrient solution	Plants surviving	Grain		Entire plants	
		Dry weight	Relative dry weight	Dry weight	Relative dry weight
	Number	*Grams*	*Percent*	*Grams*	*Percent*
Control	4	1,134	100	2,717	100
50-chloride	4	613	54	1,720	63
150-chloride	4	80	7	421	15
50-sulfate	4	961	85	2,213	81
150-sulfate	4	399	35	1,165	43
250-sulfate	4	150	13	586	22

ALFALFA, CHILEAN (APR. 17–OCT. 10)

Nutrient solution	Plants surviving	Hay cuttings								Roots	
		Dry weight				Relative dry weight					
		July 10	Aug. 21	Oct. 30	Total	July 10	Aug. 21	Oct. 30	Total	Dry weight	Relative dry weight
	Number	*Grams*	*Grams*	*Grams*	*Grams*	*Percent*	*Percent*	*Percent*	*Percent*	*Grams*	*Percent*
Control	15	385	201	235	821	100	100	100	100	87	100
50-chloride	13	235	158	210	603	61	79	89	73	81	93
150-chloride	11	137	107	114	358	36	53	49	44	63	72
50-sulfate	15	276	196	189	661	72	98	80	81	67	77
150-sulfate	15	232	162	176	569	60	81	75	69	62	71
250-sulfate	15	178	153	135	466	46	77	57	57	54	62

COTTON, ACALA (APR. 17–NOV. 9)

Nutrient solution	Plants tested	Seed cotton		Entire plants	
		Dry weight	Relative dry weight	Dry weight	Relative dry weight
	Number	*Grams*	*Percent*	*Grams*	*Percent*
Control	4	622	100	2,116	100
50-chloride	4	469	75	1,560	74
150-chloride	4	287	46	870	41
50-sulfate	4	492	79	1,321	62
150-sulfate	4	460	74	1,274	60
250-sulfate	4	251	40	657	31

TOMATO, STONE (APR. 17–SEPT. 20)

Nutrient solution	Plants tested	Vines (excluding fruit)		Total fruits					Entire plants	
		Dry weight	Relative dry weight	Fresh weight	Dry weight [2]	Relative dry weight	Average fresh weight (per fruit)	Number with blossom-end rot	Dry weight	Relative dry weight
	Number	*Grams*	*Percent*	*Grams*	*Grams*	*Percent*	*Grams*	*Percent*	*Grams*	*Percent*
Control	2	2,232	100	16,741	921	100	130	0	3,153	100
50-chloride	2	1,719	77	13,619	749	81	90	7	2,468	78
150-chloride	2	594	27	673	37	4	22	34	631	20
50-sulfate	2	1,764	79	12,115	666	72	148	2	2,430	77
150-sulfate	2	1,363	61	4,480	246	27	43	78	1,609	51
250-sulfate	2	771	35	1,774	98	11	25	84	869	28

[2] Assumed moisture content of fresh fruit, 94.5 percent.

TABLE 3.—*Growth and yield of plants in experiment* 1—Continued

BARLEY, CLUB MARIOT (APR. 11–JULY 31)

Nutrient solution	Plants		Grain		Entire plants	
	Tested	Average height	Dry weight	Relative dry weight	Dry weight	Relative dry weight
	Number	*Centimeters*	Grams	Percent	Grams	*Percent*
Control	12	100	[3] 214	100	564	100
50-chloride	12	88	295	138	685	121
150-chloride	12	67	104	49	219	39
50-sulfate	12	90	247	115	495	88
150-sulfate	12	75	144	67	322	57
250-sulfate	12	70	67	31	195	35

SUGAR BEETS, U. S. NO. 1 (APR. 17–OCT. 29)

Nutrient solution	Plants tested	Beets	
		Average fresh weight	Average fresh weight (relative)
	Number	*Grams*	*Percent*
Control	4	1,475	100
50-chloride	4	1,452	98
150-chloride	4	1,281	87
50-sulfate	4	1,148	78
150-sulfate	4	1,209	82
250-sulfate	4	837	59

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[3] The control barley, though systematically dusted, was heavily infested with mildew. There was little or no mildew on the other barley plants. The early growth of the control barley was more rapid than that of the other barley plants.

The lemon plants, which were from 4-inch January cuttings with two leaves, were rooted in the greenhouse in coarse sand and transplanted when the first growth cycles were making their appearance. Of the eight crops, lemon was the most sensitive to the chloride salts. The combined roots, stems, and retained leaves of the three plants supplied with solution containing 50 milliequivalents of chloride per liter weighed 28 percent as much as those of the plants in the control bed, and all of the plants in the 150-chloride bed died. The sulfate tolerance of the lemon plant was much higher than its chloride tolerance; two of the three rooted cuttings set out in the 250-sulfate bed lived until the end of the season, all of them making some growth.

Chapman and Liebig (5) in greenhouse experiments, found no depression in the growth of sweet orange seedlings from either 20 milliequivalents of chloride or 20 milliequivalents of sulfate when these ions were added as mixed salts of potassium, calcium, and magnesium in a series of solutions of different nitrate concentration.

Milo was substantially more tolerant to chloride during its early growth stages than after the approach of flowering. With the appearance of the flower stalks the leaves of plants in the 150-chloride bed began to burn, and they made poor heads, whereas the burning of milo leaves in the sulfate beds came on gradually. This observation, which was again made in a later experiment points to a chloride-induced physiological upset associated with the time of rapid translocation of materials to the flower stalks in this variety of milo. It will later be shown (tables 5 and 6) that milo in the 150-chloride bed accumulated a disproportionately high concentration of chloride ion in its sap.

Three cuttings were made from the alfalfa, and there was considerable variation in the growth depression of these successive crops in both the chloride and the sulfate series. The growth of the midsummer crop was reduced relatively less by salt than either the first or final crop.

The vegetative growth of cotton plants was reduced relatively more by chloride and sulfate salts than was the yield of seed cotton. The average weight of individual bolls was not affected by the treatments. The plants from this experiment are shown as figure 1.

Fruit production by tomatoes was depressed by salt roughly in proportion to the respective reductions in vine growth in the 50-chloride and 50-sulfate beds, but in the beds maintained with higher salt concentrations blossom-end rot became the dominant factor in yield. Blossom-end rot and its greater severity in the sulfate beds will receive consideration after the discussion of the analysis of the expressed sap.

The barley in the control bed was severely affected with mildew, but there was little or none on the plants in the salt beds. Because of the poor condition of the control barley, satisfactory conclusions cannot be drawn with respect to this plant's salt tolerance. It may be noted, however, that the reductions in yield between the 50- and 150-chloride and between the 50-, 150-, and 250-sulfate beds are proportionately much sharper than was the case with some other crops, indicating that mildew had substantially reduced the growth of the control plants. It has been observed, both in this experiment and in other experiments at this laboratory, that either chloride or sulfate salt, as well as boron (8), serves to repress mildew infestations of barley.

The sugar beets showed a high degree of tolerance to chloride but not to sulfate salts; a greater reduction in yield was found to result from 50 milliequivalents of sulfate than from 150 milliequivalents of chloride

Lill, Byall, and Hurst (16) have recently reported an increased growth of sugar beets in Michigan following applications of upward to 1,000 pounds of sodium chloride per acre. These increases were not as great as those resulting from complete fertilizers, and they were attributed to the indirect effects of thr salt in the liberation of nutritional elements from the soil.

To facilitate a comparison of the toxicity of chloride and sulfate salts to this series of plants, the means of the relative production in the 50- and 150-sulfate beds and in the 150- and 250-sulfate beds have been set opposite the relative yields in the 50-chloride bed (table 4). Under the conditions of this cxperimcnt, 50 milliequivalcnts of chloride brought about growth depressions of dwarf milo, alfalfa, and cotton that were roughly equal to those indicated for 100 milliequivalents of sulfate. The toxicity of chloride to these particular plants, as measured in milliequivalents, was thus about twice as great as the toxicity of sulfate. Navy beans withstood 100 milliequivalents of sulfate substantially better than 50 milliequivalents of chloride, and the lemon plants withstood three or four times as much sulfate ion as chloride ion. Beets, on the other hand, were nearly as sensitive as alfalfa to sulfate, but they withstood high concentrations of chloride with little injury. The tomato plants withstood 50 milliequivalents of chloride better than 100 milliequivalents of sulfate.

On the basis of the similarity in the toxicity of 50 milliequivalents of chloride and 100 milliequivalents of sulfate to milo, alfalfa, and

TABLE 4.—*Growth of plants in 50 milliequivalents of chloride and in 100 and 200 milliequivalents of sulfate (average of 50 and 150 milliequivalents and 150 and 250 milliequivalents of sulfate) relative to the control plants*

Crop	Yield[1] with indicated concentration of		
	Chloride	Sulfate	
	50 milliequivalents	100 milliequivalents	200 milliequivalents
	Percent	*Percent*	*Percent*
Lemon cuttings	28	59	24
Navy beans (seed)	39	45	----------
Dwarf milo (grain)	54	60	24
Chilean alfalfa (3 cuttings)	73	75	63
Acala cotton (seed cotton)	75	77	57
Stone tomatoes (entire)	78	64	40
Sugar beets (fresh roots)	98	80	71

[1] Percentage of yield with control nutrient solution.

cotton, it might be urged **that** if the concentrations of the chloride and sulfate salts had been measured in terms of electrical conductivity or freezing-point depression (see table 5) or in terms of moles of salt or of total solids, an equal toxicity of the two ions would have been indicated. The possibility of such simple relationships in salt toxicity is largely eliminated, however, when account is taken of the fact that two of these seven crops (lemon and navy bean) were far more tolerant, of 100 milliequivalents of sulfate than of *50* milliequivalents of chloride and that two others (tomato and sugar beet) were substantially more tolerant of *50* milliequivalents of chloride than of 100 milliequivalents of sulfate. The evidence of specific ion effects is such as to indicate that it will not be possible to satisfactorily evaluate chloride and sulfate toxicity on the basis of any of these summation indices. Furthermore, the toxicity of chloride and sulfate cannot be expected to be independent of the kind and proportions of the bases with which they are associated in culture or soil solutions.

SYMPTOMS

The leaves of lemon plant's in the control bed were larger than those in the salt beds, and the control plants were more vigorous and healthy in appearance. Nevertheless, symptoms of diagnostic value were lacking except for some yellowing, which preceded leaf abscission in both the chloride and sulfate beds and an occasional burned tip in the chloride bed. Badly injured lemon trees in San Diego County, Calif., irrigated with a water high in chloride, have been observed to show marked bronzing of the leaves, and the fruit from the grove softened badly while in the packing house. Chapman and Liebig (6) record some burning of the leaves of their orange seedlings in 20 milliequivalents of chloride, but this was not accompanied by reduced growth.

The size of the leaves of the beans in the salt beds was reduced roughly in proportion to the reduction in plant size, but, the size of the mature seeds was not affected. When harvested on July 13, the control plants and the plants in the 50-sulfate bed had a few dead leaves, but nearly all were green. Most of the leaves had burned and if still retained were nearly ready to drop from the plants in the 50-chloride and 150-sulfate beds.

There were outstanding differences at time of harvest in the amount of burning of the milo leaves under the different treatments. At this stage the oldest leaves of the control plants had already died, and the margins of the leaves successively higher up the stalk showed drying to a decreasing degree; in the 50-chloride bed, from 25 to 50 percent of the leaf tissue was dead; the drying started at the margin, but it was accompanied by some yellow striping between the veins. The milo in the 150-chloride bed was practically dead when harvested a month in advance of the five other cultures. Less than 25 percent of the leaf tissue was dead in the 50-sulfate milo bed, and about 50 percent in the 250-sulfate; the plants in the 150-sulfate bed were intermediate. The stalks of the plants in all of the beds except the 150-chloride were still green when harvested, but they had started to dry near the heads.

Except for a reduction in plant size and a tendency toward slightly smaller leaves, the alfalfa in the high-chloride and high-sulfate beds lacked outward leaf symptoms indicative of salt injury. The margins of some leaves in the salt beds turned white in a narrow band, but this symptom cannot be regarded as specific, since it has been observed in fields and in other experiments where high salt conditions did not exist. The last two crops of alfalfa began to flower irregularly earlier in the chloride- and sulfate-treated beds than in the control bed.

The cotton plants growing in the high-chloride and high-sulfate beds were reduced in size, and the leaves were somewhat smaller than the controls, but otherwise all were normal in appearance (fig. 1). Symptoms of injury or other abnormalities were lacking.

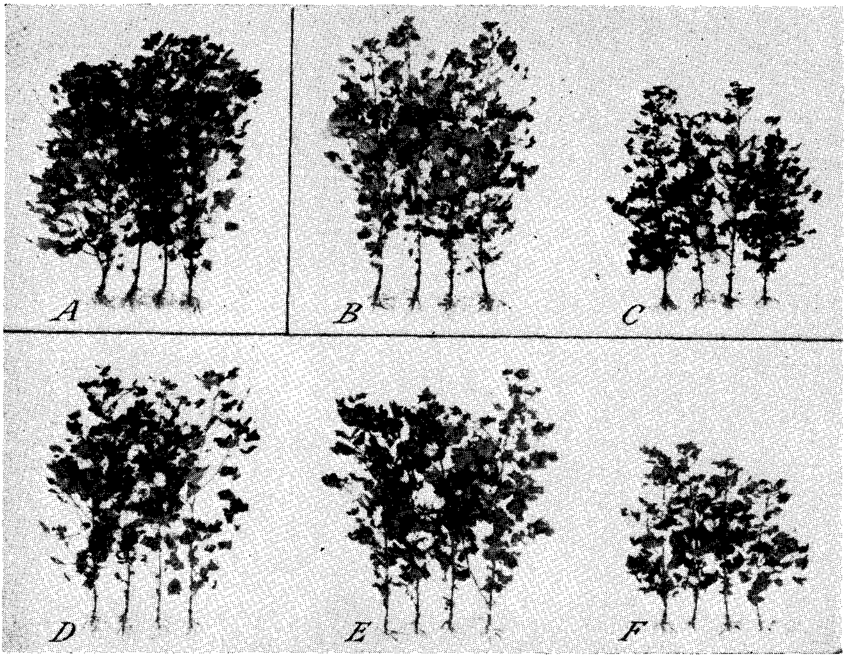

FIGURE 1.-Cotton grown in the 1934 sand-culture experiments, with various concentrations of salts added to the nutrient solution: A, Control; B, 50 milliequivalents of chloride per liter; C, 150 milliequivalents of chloride; D, 50 milliequivalents of sulfate; E, 150 milliequivalents of sulfate; and F, 250 milliequivalents of sulfate.

Aside from the prevalence of blossom-end rot on the tomatoes, neither chloride nor sulfate salts produced symptoms of injury.

The tips of older leaves of barley plants under both the chloride and sulfate treatments were burned considerably, and this burning was more pronounced with the higher concentrations.

The leaves of the beets in all beds were normal in appearance.

GROWTH-DEPRESSION GRAPHS

The character of the growth-depression graphs (fig. 2) is regarded as significant. No evidence is afforded by these graphs of a particular range of chloride or sulfate concentrations that can be regarded as critical in the sense that the term is sometimes applied in discussions of salt toxicity. Starting at some most favorable concentration, undetermined in this experiment, each additional unit of chloride and sulfate brought about further depression in growth. The graphs tend to flatten out as the concentrations become higher, indicating that the toxicity per unit of salt decreased as units were added. This latter

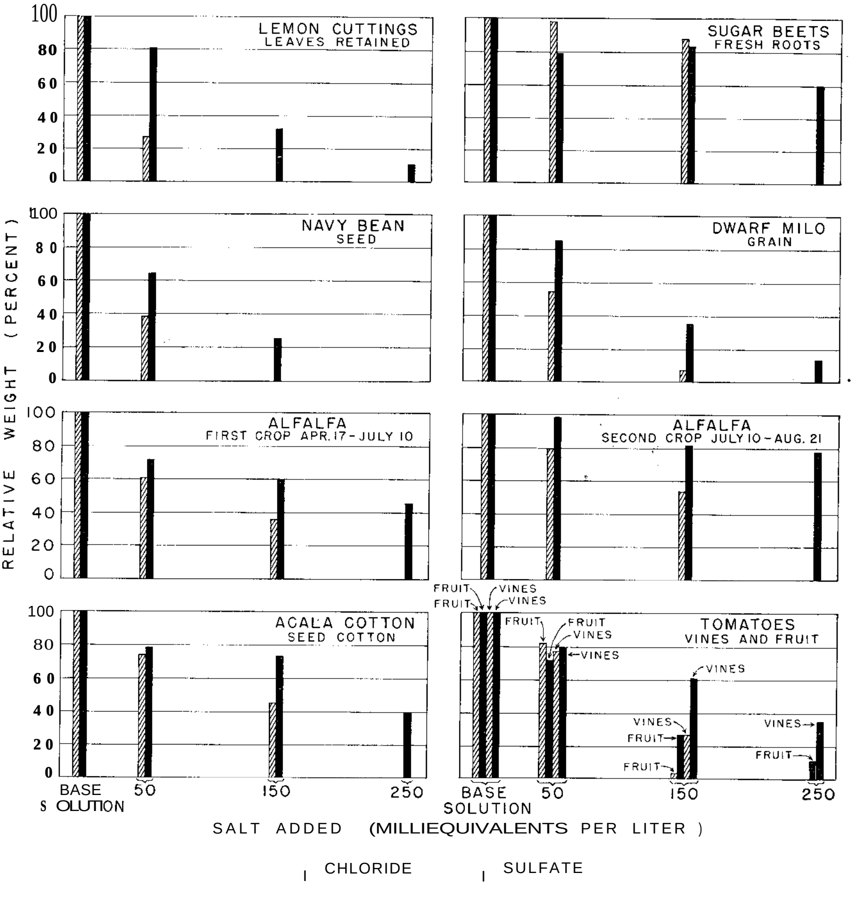

FIGURE 2.-Growth depression produced by chloride and sulfate salts. The parts of plants taken are as indicated under the names of the crops. Growth is represented relative to that of plants in the control bed.

point will be taken up again in the discussion of the analyses of plant saps and in connection with experiments conducted in water cultures in the greenhouse.

PHYSICAL AND CHEMICAL PROPERTIES OF PLANT SAP

EXTRACTION OF PLANT SAP

The samples of freshly picked leaves, or entire tops in the case of alfalfa and barley, were compacted in glass tubes, which were then stoppered and sealed with paraffin paper secured in place with rubber bands. These tubes were packed in solid carbon dioxide and allowed to stand overnight, after which the samples were thawed out one at a time, and the sap was expressed while still cold by the gradual application of pressure of 2,400 pounds per square inch in a Carver press having monel-metal parts. The samples were left at this pressure for several minutes or until the rate of sap release became very slow.

The evidence of Phillis and Mason (26) on the marked differences in the composition of the fluids expressed from flat piles of unfrozen cotton leaves (regarded as vacuolar sap) and that obtained after the residue was frozen (regarded as principally cytoplasmic sap) raises important questions as to the equilibriums existing between these leaf-tissue fluids and the extent of dissociation of the organic and inorganic materials in living cytoplasm. This question of interpretation and expressed-sap data extends further to possible differences in composition and physical characteristics between the fluids obtained from palisade, spongy parenchyma, and epidermal tissues, all of which, as shown by Turrell (33), are extensively exposed to the intercellular air spaces of the leaf. Leaving these problems and the indicated complex relations as they now stand, there still remains much justification for employing the customary methods in studies of the reaction of plants to their environment in terms of the characteristics of the composite sap obtained from frozen tissue.

EFFECT OF SALT ON SUCCULENCE

Barley was the only crop that showed a change in quantity of expressed sap with changes in the composition of the nutrient solution; both chloride and sulfate salts decreased the succulence of barley. The control and the barley plants in the 50- and 150-chloride beds yielded respectively 72, 48, and 39 ml. of sap per 100 gm. of fresh tissue, and the control and the plants in the 50-, 150-, and 250-sulfate beds yielded respectively 72, 51, 45, and 32 ml. The quantities of expressed sap from the other plants were notably uniform throughout the treatments. The average yield of sap from milo leaves was 52 ml. per 100 gm. of tissue; from alfalfa plants, 47 ml.; from cotton leaves, 67 ml.; from tomato leaflets, 71 ml.; and from sugar-beet leaf blades, 47 ml.

ACCUMULATION OF SALT CONSTITUENTS IN PLANT SAP

Determinations were made of the concentration of some or all of the following constituents in each of the sap samples: Calcium, magnesium, sodium, potassium, total sulfur, chloride, and total phosphorus. The official methods of the Association of Official Agricultural Chemists for plant materials were followed! with the exception that sodium was determined by the uranyl-zinc-acetate method and potassium by a cobaltinitrite procedure. The data on date of collection of the samples and the parts of the plants represented are given in table *8*. For purposes of discussion total sulfur and total phosphorus are treated as SO, and PO,.

The results of the sap analyses and the average composition of the nutrient solutions are presented in tables 5 and 6. In table 5 each crop is considered in turn and the effect of the added salt's is shown on the pH value, electrical conductance, and ionic concentration. In table 6 the data are so grouped as to bring out differences among the crops in the accumulation of each of the electrolytes. The first method is the more logical, but the second furnishes a better basis for discussion of the comparative reactions of the different crops. In table 6 the accumulation ratios also are shown. The term "accumulation ratio," as here used, signifies the concentration of a constituent in expressed plant sap divided by the concentration in the supporting nutrient solution, i. e., the concentration gradient against which additional small quantities of the ion would be accumulated. Eight different crops were grown in the beds, but there was insufficient material for sap analyses of the lemons and navy beans, and only partial analyses were made of the barley. The agricultural plants used for the salt-uptake comparisons (table 5) represent five well-differentiated botanical families, namely, the Gramineae (two representatives), the Leguminosae, the Malvaceae, the Solanaceae, and the Chenopodiaceae.

Certain important similarities of reaction to the added salts have been found among these six crop plants, but on first appraisal diversity of behavior and species specificity are the prominent features. The data well illustrate the hazards associated with the formulation of generalizations on ionic uptake and interionic effects on the basis of the reactions of a single plant species.

All crops accumulated relatively high concentrations of cations from the base nutrient solution (table *6)*, but the concentrations in milo, for example, were only approximately one-half as great, on all solutions as those in cotton. The concentration of total bases in the sap of milo and cotton in the control bed was, respectively, *18.2* and *34.8* times as great as in the nutrient solution. Alfalfa, tomatoes, and sugar beets occupied intermediate positions. The total concentration and, in most instances, the concentration of individual ions in the sap were greater in plant's grown in the salt beds than in the control bed, but it is to be noted that the accumulation ratios decreased with the addition of salt. The milo and cotton, with accumulation ratios of 18.2 and 34.8, respectively, for total bases in the control bed, had ratios of **1.8** and 3.5, respectively, in the 250-sulfate bed.

The sharp decreases in accumulation ratios with the addition of ions to the nutrient have shown the need of an additional measure of the effects of substrate concentrations upon the accumulation of salt in plants. To this end there are set forth in table 7 what are termed "increment ratios." These values represent the ratios of the differences in the concentration of the ions in the sap of the salt-treated and the control plants divided by the differences between the saline and control solutions:

$$\text{Increment ratio}=\frac{\text{sap concentration of salt-treated plant-sap concentration of control plant}}{\text{solution concentration in salt bed--solution concentration in control bed}}$$

TABLE 5.—*Concentration of inorganic constituents in expressed plant sap and in supporting nutrient solutions of various crops (experiment 1, 1934)*

Nutrient solution and source of sap	pH	Freezing-point depression (°C.)	Conductance ($K \times 10^5$ at 25° C.)	Constituent (milliequivalents per liter)								
				Ca	Mg	Na	K	Sum	Cl	Total S as SO_4	Total P as PO_4	NO_3
Culture solutions (average new and discarded):												
Control	7.2	0.06	172	5.49	2.26	3.78	5.84	17.4	0.58	2.68	[1] 0.15	7.79
50-chloride	7.2	.21	665	17.72	14.73	27.40	6.81	66.7	51.21	2.93	.13	8.58
150-chloride	7.1	.50	1,620	42.44	41.56	77.70	8.06	169.8	149.33	3.26	.15	11.03
50-sulfate	7.1	.15	531	16.41	15.29	25.55	7.01	64.3	.90	50.02	.14	8.34
150-sulfate	7.2	.29	1,096	23.58	58.59	73.55	7.56	163.3	.74	147.47	.18	9.43
250-sulfate	7.2	.42	1,603	25.14	105.40	120.43	8.02	259	.82	241.29	.29	11.08
Milo, dwarf (leaves):												
Control	4.72	.92	1,690	63	74	1	179	316	26	21	------	------
50-chloride	4.63	1.11	1,868	96	144	4	155	399	81	------	------	------
150-chloride	4.38	1.49	2,731	151	210	14	180	555	267	------	------	------
50-sulfate	4.68	1.04	1,732	57	100	5	180	342	35	------	------	------
150-sulfate	4.57	1.10	1,821	44	179	9	194	426	27	45	------	------
250-sulfate	4.56	1.15	1,821	42	216	13	203	474	------	110	------	------
Alfalfa (first cutting):												
Control	5.31	.95	1,628	125	16	8	167	316	------	47	------	------
50-chloride	5.25	1.06	1,776	158	47	14	112	331	------	27	------	------
150-chloride	5.13	1.28	2,093	151	69	31	109	360	------	43	------	------
50-sulfate	5.28	1.03	1,724	109	55	15	149	328	------	49	------	------
150-sulfate	5.25	1.29	1,953	88	96	18	164	366	------	82	------	------
250-sulfate	5.32	1.41	1,831	71	142	35	163	411	15	142	------	------
Alfalfa (second cutting):												
Control	----	1.26	2,284	128	68	15	342	551	------	------	------	------
50-chloride	----	1.26	2,372	121	76	32	306	535	84	------	------	------
150-chloride	----	1.41	2,428	118	94	32	297	541	130	------	------	------
50-sulfate	----	1.15	2,097	80	64	32	286	462	21	------	------	------
150-sulfate	----	1.14	1,891	56	89	58	250	453	19	------	------	------
250-sulfate	----	1.37	2,156	55	159	80	240	534	17	------	------	------
Alfalfa, third cutting (stems and leaves):												
Control	---	1.23	2,149	107	62	25	265	459	25	38	33	------
50-chloride	---	1.28	2,324	109	74	39	250	472	79	31	30	------
150-chloride	----	1.47	2,753	133	98	65	230	526	171	33	33	------
50-sulfate	----	1.27	2,135	90	70	53	255	468	27	45	30	------
150-sulfate	----	1.31	2,179	58	100	81	243	482	20	67	42	------
250-sulfate	----	1.43	2,359	49	156	121	224	550	17	118	46	------
Cotton, Acala (leaves):												
Control	----	1.15	2,024	251	108	18	228	605	18	183	7	------
50-chloride	----	1.19	2,211	335	134	26	185	680	76	230	7	------
150-chloride	----	1.31	2,716	427	165	27	132	751	178	232	5	------
50-sulfate	----	1.15	2,165	358	141	25	255	779	9	328	7	------
150-sulfate	----	1.16	2,382	352	223	38	208	821	4	392	9	------
250-sulfate	----	1.23	2,692	334	283	51	240	908	2	439	9	------
Tomato (leaves):												
Control	----	.79	1,886	115	83	6	161	365	25	150	26	------
50-chloride	----	.90	2,179	164	130	11	129	434	71	152	20	------
150-chloride	----	1.18	2,724	205	130	14	154	503	155	128	24	------
50-sulfate	----	.89	2,101	89	111	15	177	392	23	177	24	------
150-sulfate	----	1.01	2,147	315	68	17	165	565	17	222	27	------
250-sulfate	----	1.14	2,354	478	63	28	153	722	13	299	------	------
Barley (stems, leaves, and flowering heads):												
Control	6.01	.83	2,438	------	------	------	------	------	63	16	------	------
50-chloride	5.99	1.24	2,882	------	------	------	------	------	168	21	------	------
150-chloride	5.66	1.72	3,963	------	------	------	------	------	347	22	------	------
50-sulfate	6.00	1.50	2,642	------	------	------	------	------	89	26	------	------
150-sulfate	6.02	1.39	3,019	------	------	------	------	------	96	73	------	------
250-sulfate	6.02	1.57	3,170	------	------	------	------	------	91	116	------	------
Sugar beets (leaves):												
Control	5.97	1.13	2,964	(2)	101	229	167	497	44	40	23	------
50-chloride	5.95	1.36	3,392	(2)	145	297	192	634	91	29	17	------
150-chloride	5.96	1.75	4,126	(2)	167	392	187	746	175	41	17	------
50-sulfate	5.93	1.31	3,180	(2)	103	258	190	551	31	55	17	------
150-sulfate	5.95	1.41	3,318	(2)	130	370	120	620	43	82	15	------
250-sulfate	5.99	1.40	3,550	(2)	104	347	158	609	44	110	13	------

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[1] Average of used solutions only. There was a heavy precipitation of phosphate when new solutions were first applied.

[2] Trace.

The concentrations of constituents in the sap of plants growing in the salt beds were in some instances found to be lower than those in the sap of control plants; these reductions in concentration are indicated by —c. Ratios below unity show that the sap concentration of the salt plant was greater than that of the control plant but that the

TABLE 6.—*Concentrations and accumulation ratios of inorganic constituents in nutrient solutions and plant saps*

Treatment	(A) Concentration (milliequivalents per liter)						(B) Accumulation ratio (sap concentration/solution concentration)					
	Control bed	Chloride bed		Sulfate bed			Control bed	Chloride bed		Sulfate bed		
		50 milliequivalents	150 milliequivalents	50 milliequivalents	150 milliequivalents	250 milliequivalents		50 milliequivalents	150 milliequivalents	50 milliequivalents	150 milliequivalents	250 milliequivalents
Total cations:												
Culture solution	17.4	66.7	169.8	64.3	163.3	259	------	------	------	------	------	------
Expressed sap:												
Milo	316	399	555	342	426	474	18.2	6.0	3.3	5.3	2.6	1.8
Alfalfa (third cutting)	459	472	526	468	482	550	26.4	7.1	3.1	7.3	3.0	2.1
Cotton	605	680	751	779	821	908	34.8	10.2	4.4	12.1	5.3	3.5
Tomato	365	434	503	392	565	722	21.0	6.5	3.0	6.1	3.5	2.8
Sugar beet	497	634	746	551	620	609	28.6	9.5	4.4	8.6	3.8	2.4
Calcium:												
Nutrient solution	5.5	17.7	42.4	16.4	23.6	25.1	------	------	------	------	------	------
Expressed sap:												
Milo	63	96	151	57	44	42	11.5	5.4	3.6	3.5	1.9	1.7
Alfalfa (third cutting)	107	109	133	90	58	49	19.5	6.2	3.1	5.5	2.5	2.0
Cotton	251	335	427	358	352	334	45.6	18.9	10.1	21.8	14.9	13.3
Tomato	115	164	205	89	315	478	20.9	9.3	4.8	5.4	13.3	19.0
Sugar beet	(1)	(1)	(1)	(1)	(1)	(1)	------	------	------	------	------	------
Magnesium:												
Nutrient solution	2.3	14.7	41.6	15.3	58.6	105.4	------	------	------	------	------	------
Expressed sap:												
Milo	74	144	210	100	179	216	32.2	9.8	5.0	6.5	3.1	2.0
Alfalfa (third cutting)	62	74	98	70	100	156	27.0	5.0	2.4	4.6	1.7	1.5
Cotton	108	134	165	141	223	283	47.0	9.1	4.0	9.2	3.8	2.7
Tomato	83	130	130	111	68	63	36.1	8.8	3.1	7.3	1.2	.6
Sugar beet	101	145	167	103	130	104	43.9	9.9	4.0	6.7	2.2	1.0
Sodium:												
Nutrient solution	3.8	27.4	77.7	25.6	73.6	120.4	------	------	------	------	------	------
Expressed sap:												
Milo	1	4	14	5	9	13	.3	.2	.2	.2	.1	.1
Alfalfa (third cutting)	25	39	65	53	81	121	6.6	1.4	.8	2.1	1.1	1.0
Cotton	18	26	27	25	38	51	4.7	1.0	.4	1.0	.5	.4
Tomato	6	11	14	15	17	28	1.6	.4	.2	.6	.2	.2
Sugar beet	229	297	392	258	370	347	60.3	10.8	5.0	10.1	5.0	2.9
Potassium:												
Nutrient solution	5.8	6.8	8.1	7.0	7.6	8.0	------	------	------	------	------	------
Expressed sap:												
Milo	179	155	180	180	194	203	30.9	22.8	22.2	25.7	25.7	25.4
Alfalfa (third cutting)	265	250	230	255	243	224	45.7	36.8	28.4	36.4	32.0	28.0
Cotton	228	185	132	255	208	240	39.3	27.2	16.3	36.4	27.4	30.0
Tomato	161	129	154	177	165	153	27.8	19.0	19.0	25.3	21.7	19.1
Sugar beet	167	192	187	190	120	158	28.8	28.2	23.1	27.1	15.8	19.8
Chloride:												
Nutrient solution	.6	51.2	149.3	.9	.7	.8	------	------	------	------	------	------
Expressed sap:												
Milo	26	81	267	35	27	------	43.3	1.6	1.8	38.9	38.6	------
Alfalfa (third cutting)	25	79	171	27	20	17	41.7	1.5	1.1	30.0	28.6	21.3
Cotton	18	76	178	9	4	2	30.0	1.5	1.2	10.0	5.7	2.5
Tomato	25	71	155	23	17	13	41.7	1.4	1.0	25.6	24.3	16.3
Sugar beet	44	91	175	31	43	44	73.3	1.8	1.2	34.4	61.4	55.0
Sulfate:												
Nutrient solution	2.7	2.9	3.3	50	147.5	241.3	------	------	------	------	------	------
Expressed sap:												
Milo	21	------	------	------	45	110	7.8	------	------	------	.3	.5
Alfalfa (third cutting)	38	31	33	45	67	118	14.1	10.7	10.0	.9	.5	.5
Cotton	183	230	232	328	392	439	67.8	79.3	70.3	6.6	2.7	1.8
Tomato	150	152	128	177	222	299	55.6	52.4	38.8	3.5	1.5	1.2
Sugar beet	40	29	41	55	82	110	14.8	10.0	12.4	1.1	.6	.5

---

[1] Trace.

increment was less than the quantity added to the base nutrient. Values above unity show the extent to which sap accumulations exceeded the additions to the solutions.

In contrast to the high accumulation ratios found in the control bed, sodium excepted, the increment ratios are usually low; the values are more often below unity than above. Except for the sugar beets in all salt beds and alfalfa in the 50-sulfate bed, no plant increased the sodium concentration in its sap by as much as the solution was increased. Noteworthy is the fact that the chloride increments in the sap of all plants in the two chloride beds were approximately equal to the increments added to the solutions; except for the milo in the 150-chloride bed, no chloride-increment ratio exceeded 1.2

TABLE 7.—*Concentrations and increments of ions in culture solutions, and corresponding accumulation ratios and increment ratios*[1][2] *in sap of crop plants (experiment 2)*

Ion and nutrient solution	Culture solution		Milo		Alfalfa		Cotton		Tomato		Sugar beet	
	Concentration	Increment	Accumulation ratio	Increment ratio	Accumulation ratio	Increment ratio	Accumulation ratio	Increment ratio	Accumulation ratio	Increment ratio	Accumulation ratio	Increment ratio
	Milliequivalents	*Milliequivalents*										
Total cations:												
Control	17.4		18.2		26.4		34.8		21.0		28.6	
50-chloride		49.3		1.7		0.3		1.5		1.4		2.8
150-chloride		152.4		1.6		.4		1.0		.9		1.6
50-sulfate		46.9		.6		.2		.4		.6		1.2
150-sulfate		145.9		.8		.2		1.5		1.4		.8
250-sulfate		241.6		.7		.4		1.3		1.5		.5
Calcium:												
Control	5.5		11.5		19.5		45.6		20.9			
50-chloride		12.2		2.7		.2		6.9		4.0		
150-chloride		36.9		2.4		.7		2.5		2.4		
50-sulfate		10.9		−c		−c		9.8		−c		
150-sulfate		18.1		−c		−c		5.6		11.1		
250-sulfate		19.6		−c		−c		4.2		18.5		
Magnesium:												
Control	2.3		32.2		27.0		47.0		36.1		43.9	
50-chloride		12.4		5.7		1.0		2.1		3.8		3.6
150-chloride		39.3		3.5		.9		1.5		1.2		1.7
50-sulfate		13.0		2.0		.6		2.5		2.2		.2
150-sulfate		56.3		1.9		.7		2.0		−c		.5
250-sulfate		103.1		1.4		.9		1.7		−c		0
Sodium:												
Control	3.8		.3		6.6		4.7		1.6		60.3	
50-chloride		23.6		.1		.6		.3		.2		2.9
150-chloride		73.9		.2		.5		.1		.1		2.2
50-sulfate		21.8		.2		1.3		.3		.4		1.3
150-sulfate		69.8		.1		.8		.3		.2		2.0
250-sulfate		116.6		.1		.8		.1		.2		1.0
Chloride:												
Control	.6		43.3		41.7		30.0		41.7		73.3	
50-chloride		50.6		1.1		1.1		1.2		.9		.9
150-chloride		148.7		1.6		1.0		1.1		.9		.9
50-sulfate		.3										
150-sulfate		.1										
250-sulfate		.2										
Sulfate:												
Control	2.7		7.8		14.1		67.8		55.6		14.8	
50-chloride		.2										
150-chloride		.6										
50-sulfate		47.3				.2		3.1		.6		.3
150-sulfate		144.8		.2		.2		1.4		.5		.3
250 sulfate		238.6		.4		.3		1.1		.6		.3

[1] Increment ratio $=\frac{\text{sap concentration of salt-treated plant} - \text{sap concentration of control plant}}{\text{solution concentration in salt bed} - \text{solution concentration in control bed}}$

[2] −c indicates a concentration in sap of salt plant less than that in sap of control plant.

and none fell below 0.9. In other words, with the addition of either 50 or 150 milliequivalents of chloride to the base solution, which contained 0.6 milliequivalent, each of these five botanically distinct plants increased the concentration of chloride in its sap by quantities nearly equal to the additions to the culture solutions. In other experiments, not included in this report, chloride-increment ratios that departed further from unity have been observed, and climatic variables may have an important influence. The growth of most of these plants was markedly reduced with these higher chloride levels in the sap, but the fact that the growth of beets was affected but little is to be especially noted as an indication of the great diversity in the responses of different plants to similar accumulations. The relatively low increment ratios for nearly all ions and plants as here found probably constitute one of the most important points to be considered in any study of the reactions of plants on saline substrates.

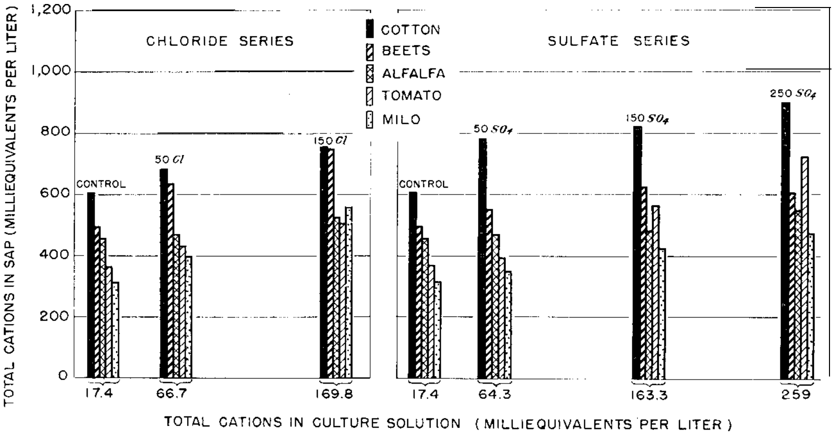

FIGURE 3.--Accumulation of total bases in the sap of plants grown in the control solution and in the chloride and sulfate solutions.

In figure 3, total bases in the plant saps are plotted against the total bases in the corresponding culture solutions. The concentration of total bases in the nutrient solution of the control bed was 17.4 milliequivalents per liter. The tenfold increase in the concentration of bases in the solution serving the high-chloride bed or the fourteenfold increase in the high-sulfate bed in no instance served to double the concentrations of total bases in the expressed sap of any of these plants.

When the accumulations of the individual bases in table 6 are examined, much specificity is found to exist. The sap of the sugar beet, for example, in harmony with the observation of McCool and Weldon (20), contained little or no calcium, although this plant has not been found abnormal when calcium determinations were made on dry leaf tissue. Cotton and tomatoes, on the other hand, tend to maintain a high calcium concentration. The tomato plants accumulated far more calcium from solutions high in chloride than from those high in sulfate, whereas with cotton the opposite relationship was found. Calcium accumulation is thus not independent of the kind of anion with which it is supplied.

The evidence of a correlation between accumulation of calcium and magnesium, which Collander (6) mentions, is least apparent in the sap of this series of plants; calcium and magnesium accumulations do tend to parallel one another in the chloride series, though in different, amounts, but in tho sulfate series an accumulation of one is most often associated with a depression of the other. Comparisons of the sap of the five species of plants grown in the control bed show little correlation between their calcium and magnesium content.

A notably wide variation is shown by different plant species in the extent to which they accumulate sodium. The sodium accumulation ratios (table 6, B) of milo, alfalfa, cotton, and tomatoes were very low. The beet, on the other hand, accumulated sodium in high concentrations under all the treatments. Sodium uptake was influenced by the concentration of sodium in thr culture solutions, and it made little difference whether it was added as the chloride or sulfate salt. There is little if any evidence of interrelations between sodium and potassium accumulation, but in more recent work with barley sodium accumulation has been found to depress potassium accumulation. Van Itallie *(34)* found little sodium in the sap of wheat and potatoes and much in the sap of mustard and mangcls. Collander (6) also found a great diversity in sodium uptake among plants.

It is to be observed that only a few major changes in the accumulation of potassium in the sap of these plants resulted from upward to an eightfold increase in the concentration of calcium in the nutrient solution, a forty-fivefold increase in magnesium, a thirtyfold increase in sodium, a 250-fold increase in chloride, or a ninetyfold increase in sulfate. The most important exceptionwas the depression in potassium uptake by the cotton grown in the 50-chloride and 150-chloride beds, but, no such depression occurred from thr sulfate additions. The uniformity of potassium uptake as between crops is likewise noteworthy when account is taken of the highly preferential absorption **shown** by these crops for different ones of the other ions present in solution. Van Itallie *(34) has* recently pointed to a similar uniformity in potash accumulation by a series of eight crops grown on a soil with and without sodium and sodium plus potassium additions. Van Itallie's results, which were all referred to the nitrogen found in the tissues, showed a marked variability between plants in the accumulation of cations other than potassium. Collander (6) likewise found among plants greater uniformity in potassium than in sodium or average accumulations.

With an average concentration of 0.6 milliequivalent of chloride in the base nutrient solution of thecontrol bed (table 6), from 18 to 44 milliequivalents was found in the sap of the five crops. With the addition of 50 and 150 milliequivalents of chloride to the solution there tended to be equivalent increases in the sap concentration. In other words, the increments in the sap tended to equal the increments in the solution. Milo in the 150-chloride bed was an exception.

Cotton and tomatoes throughout all treatments carried in their sap several times as much sulfur as milo, alfalfa, or sugar beets. The concentration of sulfur found in the sap of cotton in the high-sulfate bed corresponds to that of a 0.44-normal sulfate solution.

Phosphate determinations were made on only four sets of sap samples. These data show that between plants such as alfalfa and cotton (table 5) there are substantial differences in phosphate concentrations, but these concentrations were not influenced to any major extent by the uptake of other ions. The accumulation ratios were in all cases relatively high.

The pH values of the sap of some of these crops were lower for plants grown on solutions high in chloride than for those grown in the control bed; the effect is shown by milo, alfalfa, and barley, but no change was shown by beets. Sulfate had little if any effect on the hydrogen-ion concentration in the sap. All of the pH measurements were made with a glass electrode.

In another experiment, dried samples of tomato leaves collected at the end of the growth period, when analyzed for chloride and sulfate and compared with the analyses of sap samples collected 11 days earlier, showed similar relative effects of the added salt on accumulation in the leaves. The concentrations of chloride found in the dried leaf blades were somewhat lower than in the petiole and stem tissues, but the concentrations of sulfur in the dried leaves were almost six times as great as in the combined stems and petioles.

ELECTRICAL CONDUCTIVITY OF PLANT SAP

The electrical conductivities of all of the sap samples are reported in table 5. It has long been known that the conductivity of a pure solution of an inorganic electrolyte is markedly influenced by the addition of an organic substance such as sugar, and that the interpretation of conductivities of plant sap in terms of concentrations of electrolytes is highly hazardous. Greathouse *(12),* in a recent paper on conductivity measurements of plant saps, has reviewed the conclusions of a number of investigators on this subject, adding additional material from his own investigations; he lists among factors affecting conductivity values of biological solutions such things as hydration of colloids and crystalloids (bound water), viscosity, ionic adsorption, and the surface conductance of colloids. The data here presented further illustrate the complex situation that is presented by conductivity measurements made on liquids expressed from frozen plant tissues.

As the concentration of nitrate in these expressed saps was not determined, the data of table 5 cannot be fully examined for correlations between total electrolytes and conductivity. Total cations, however, provide a basis for comparison since each cation must be balanced by an anion, either organic or inorganic. It is found that a fair degree of parallelism exists between conductivity and total cations through this series of sap samples, but an entirely different situation is presented when the conductivities and total cations of the saps are compared with those of the culture solutions. This effect of the organic constituents in warping conductivity values may be illustrated by comparing the electrical conductance ($1,620 \times 10^{-5}$) of the 150-chloride culture solution and that of the sap of the milo plants in the control bed, which had a conductance of $1,690 \times 10^{-5}$. The former had by analysis 169.8 milliequivalents of bases and the latter 316.

FREEZING-POINT DEPRESSION OF PLANT SAP AND DIFFERENTIALS BETWEEN SAP AND SUBSTRATE

Data on the freezing-point depressions of the culture solutions and of the expressed sap of this series of plants are included in table 5.

The diversity shown between species recalls to mind that found by Harris and his associates (13) among native species in each of a number of associations in the Tooele Valley, Utah. In the control bed tomato was low, with a freezing-point depression of 0.79’ C., and the second cutting of alfalfa was high, with a value of **1.26’.** The subject of primary interest in the present connection, however, has to do with the corresponding changes in the plant sap and the culture solutions.

With each addition of chloride or sulfate salt to the base nutrient solution there was in general an increase in the osmotic pressure of the expressed sap. These increases in the freezing-point depression of the sap tended to parallel the corresponding increases in the freezing-point depression of the culture solutions (table 8). In some instances the sap increases exceeded the increases in the solutions and in other instances they fell below. If the six crops are viewed collectively, by means of averages? the gains in differentials are balanced by losses, which would indicate little basis for a generalization that plants on saline soils are at a disadvantage in their water relations. The view has sometimes been expressed that plants are injured by salt because of the high osmotic pressure in soil solutions and the consequent limitation to water uptake. Such a view fails to take account of the salt uptake by the plant and the tendency here shown toward the establishment of an equilibrium between the plant and its substrate; but one must not lose sight of the fact that in some of these cases there is a loss of differential with the addition of salt, which suggests that at higher concentrations water uptake

TABLE 8.—*Freezing-point depression of expressed sap of various plants* and of *the corresponding culture solutions*

FREEZING-POINT DEPRESSION

Source	Date	Portion of plant	Control	Chloride		Sulfate		
				50 milli-equivalents	150 milli-equivalents	50 milli-equivalents	150 milli-equivalents	250 milli-equivalents
			° C.	° *C.*	° *C.*	° *C.*	° *C.*	° C.
Culture solution			0.06	0.21	0.50	0.15	0.29	0.42
Milo	July 16	6th leaf from base of each plant.	.92	1.11	1.49	1.04	1.10	1.15
Alfalfa	[1]	Entire stems and leaves.	1.14	1.26	1.37	1.15	1.25	1.40
Cotton	Nor. 6	Mature and sound main-stalk leaves.	1.15	1.19	1.31	1.15	1.10	1.28
Tomato	Sept. 9	Mature leaflets	.79	.90	1.18	.89	1.01	1.14
Barley	July 5	Entire plants at thick-dough stage.	x.3	1.24	1.72	1.50	1.39	1.57
Sugar beet	Oct. 23	Sound mature leaf blades.	1.13	1.36	1.75	1.31	1.41	1.40

OSMOTIC DIFFERENTIALS BETWEEN SAP AND SOLUTION

Source	Date	Portion of plant	Control	Chloride 50 milli-equivalents	Chloride 150 milli-equivalents	Sulfate 50 milli-equivalents	Sulfate 150 milli-equivalents	Sulfate 250 milli-equivalents
			Atm.	*Atm.*	*Atm.*	*Atm.*	*Atm.*	*Atm.*
Milo			10.3	10.8	11.1	10.7	JO.4	8.8
Alfalfa			13.0	12.6	10.4	12.1	11.5	11.8
Cotton			13.1	11.8	9.7	12.1	10.4	.97
Tomato			8.8	8.3	8.2	8.9	8.6	8.6
Barley			9.2	12.4	14.7	18.2	13.2	13.8
Sugar beet			12.8	13.8	15.0	13.9	13.4	11.8
Average			11.2	11.6	11.5	12.3	11.2	10.8

[1] Average of 3 crops harvested July 9, Aug. 21, and Oct. 10.

might be appreciably slowed down provided the plants were otherwise able to tolerate the accumulated ions. No differential of less than 8 atomospheres, however, was found between the osmotic pressure of the expressed sap and the supporting culture solution in this experiment. Freezing-point depressions in degrees centigrade are related to osmotic pressures in atmospheres by the factor $12.06\Delta - 0.02\Delta^2$. Data of like character were found in experiments with wheat and Australian saltbush (7) grown on soils to which sodium chloride was added in successively larger amounts.

Although experimental data as specific as the foregoing do not appear elsewhere in the literature, it has frequently been stated that plants on saline soils have a higher salt concentration in their tissues than those on less saline soils. Such relations have been pointed to by Maximov (22) as a basis for his comment that the concept of physiological dryness of saline soils is to be regarded in a relative rather than an absolute sense. The water relations of plants in equilibrium with a saline substrate must, in the writer's opinion, be carefully differentiated from the wilting that is produced when salt or sugar is suddenly added to soils or solutions or when saline crusts are washed into the root zone by a shower. Wilting, in the few instances in which it was observed in these experiments, was always as pronounced in the control bed as in any of the salt beds.

WATER REQUIREMENTS

The water requirements of the combined plants in each of the beds are reported in table 9. Decreased water requirements were found for the 50-chloride and 50-sulfate beds, and water requirements higher than those of the controls were found for the 150-chloride and 250-sulfate beds. Increased sap concentrations are conducive to reduced transpiration rates (7), but because of the reduction in growth caused by salt, exposure to light and wind was increased, and this resulted in increased transpiration; transpiration in this experiment was thus influenced by two oppositely directed factors. Growth, measured as dry matter produced, enters into the water-requirement calculation as the denominator of the ratio in which transpiration is the numerator, and the salt and water relations as measured by water requirements are accordingly somewhat complicated.

TABLE 9.—*Water requirements of eight crops grown together in sand beds*

Nutrient solution	Total dry weight of plants	Total water lost [1]	Water per gram of dry material
	Grams	*Liters*	*Grams*
Control	11,472	6,434	561
50-chloride	8,724	4,511	517
150-chloride	3,677	2.375	646
50-sulfate	8,910	4,785	537
150-sulfate	6,270	3,513	560
250-sulfate	3,658	2,377	650

[1] Includes both transpiration by the plants and evaporation from the beds.

BLOSSOM-END ROT OF TOMATOES

The subject of blossom-end rot of tomatoes is somewhat irrelevant to the principal topic of this paper, but, as shown in table 3, this disorder, absent from the control bed, became a factor of importance in plant growth in the chloride and sulfate beds, particularly in the latter. In the 250-sulfate bed, 84 percent of the fruit was affected. The related data on the incidence of blossom-end rot and the composition of the expressed sap have been brought together in table 10.

TABLE 10.-Incidence of *blossom-end rot of tomatoes (grown* **in** sand *beds) in* relation *to calcium accumulation in leaf sap*

Nutrient solution	Fruits affected with blossom-end rot	Electrolytes in leaf sap (milliequivalents per liter)						Freezing-point depression	
		Calcium	Magnesium	Sodium	Potassium	Chloride	Sulfate	Sap from mature leaves	Differentials between solutions and mature leaves
	Percent							°*C.*	°*C.*
Control	0	115	83	6	161	25	150	0.79	0.73
50-chloride	7	164	130	11	129	71	152	.90	.69
150-chloride	34	205	130	14	154	155	128	1.18	.68
50-sulfate	78	89	111	15	177	23	177	.89	.74
150-sulfate	84	478 315	68	17	165	17	222	1.01	.72
250-sulfate			63	28	153	13	299	1.14	.72

Blossom-end rot of tomatoes has been found to develop under diverse cultural conditions, and it has been associated with a number of environmental factors; Robbins (28) has recently reviewed a part of the literature on this disease. From his own work with plants grown on nutrient solutions of varied concentration, he concluded that unfavorable osmotic pressure in fruit relative to that in vegetative shoots, causing water withdrawal and tissue break-down could be assigned as a cause.

On the basis of the observations made possible by the present experiments, it appears that neither unfavorable osmotic relations between the plants and solutions nor the accumulation of potassium or sodium can be assigned as a direct cause of the blossom-end rot induced by the treatments. Although the possibility, that high chloride and high sulfate were independent causes cannot bc entirely eliminated, the data suggest that calcium and magnesium accumulation singly or combined were important contributing factors.

The reasoning, applicable at least to this experiment, that seems to cast doubt on high osmotic pressure in the leaves and consequent unfavorable water relations in fruit's as a cause of blossom-end rot, has to do in part with the fact that only 34 percent of the fruits were affected in the high-chloride bed, where the freezing-point depression was 1.18°C in the expressed leaf sap, whereas in the 150-sulfate bed there was 78 percent of rot and a freezing-point depression of only 1.01°. As shown in table 10, there was little difference in the osmotic differentials between culture solutions and the leaves of tomatoes in any of the beds. Wilting of the tomatoes was not observed in any of the beds, but if incipient wilting did occur at any time as a result of insufficient moisture the chances for its occurrence would be greater in the control bed, from which there was greater water loss and in which there was no blossom-end rot.

For the leaves to withdraw water from the fruits it would bc necessary to assume a water deficit in the leaves since, irrespective of osmotic differentials, a turgid cell is limited in its expansion and water uptake by the cell wall which bounds the protoplast. In other words, it would not be reasonable to assume that a significant amount of water could be withdrawn from fruits by turgid leaf cells.

PLANT INJURY IN RELATION TO SALT ACCUMULATION

As shown in table 3, the addition of chloride and sulfate salts to the base nutrient resulted in a depression in the growth of nearly all plants and, as shown in tables 5 and 6, in the accumulation of chloride and sulfate in the sap in excess of the concentrations found in the control plants. With these increases in the concentration of chloride and sulfate in the plants there were also important changes in the concentration of the bases. As an aid to the reexamination of these data for causal relationships, the most pertinent of the material in these tables has been reassembled in table 11.

TABLE 11.—*Growth reductions and corresponding concentrations of chloride, sulfate, sodium, and total cations in expressed sap of six plants grown in outdoor sand beds with chloride and sulfate salts*

Crop plant and nutrient solution	Growth reduction (percentage of entire plant)	Expressed sap				
		Accumulation (milliequivalents per liter) of—				pH
		Chloride	Sulfate	Sodium	Total cations	
Milo:						
Control	0	26	21	1	316	4.72
50-chloride	37	81	----------	4	399	4.63
150-chloride	85	267	----------	14	555	4.38
50-sulfate	19	----------	----------	5	342	4.68
150-sulfate	57	----------	45	9	426	4.57
250-sulfate	78	----------	110	13	474	4.56
Alfalfa (third cutting):						
Control	0	25	38	25	459	[1] 5.31
50-chloride	11	79	----------	39	472	[1] 5.25
150-chloride	51	171	----------	65	526	[1] 5.13
50-sulfate	20	----------	45	53	468	[1] 5.28
150-sulfate	25	----------	67	81	482	[1] 5.25
250-sulfate	43	----------	118	121	550	[1] 5.32
Cotton:						
Control	0	18	183	18	605	----------
50-chloride	26	76	----------	26	680	----------
150-chloride	59	178	----------	27	751	----------
50-sulfate	38	----------	328	25	779	----------
150-sulfate	40	----------	392	38	821	----------
250-sulfate	69	----------	439	51	908	----------
Tomato:						
Control	0	25	150	6	365	----------
50-chloride	22	71	----------	11	434	----------
150-chloride	80	155	----------	14	503	----------
50-sulfate	23	----------	177	15	392	----------
150-sulfate	49	----------	222	17	565	----------
250-sulfate	72	----------	299	28	722	----------
Sugar beet (fresh roots):						
Control	0	44	40	229	497	5.97
50-chloride	2	91	----------	297	634	5.95
150-chloride	13	175	----------	392	746	5.96
50-sulfate	22	----------	55	258	551	5.93
150-sulfate	18	----------	82	370	620	5.95
250-sulfate	41	----------	110	347	609	5.99
Barley:						
Control	----------	63	----------	----------	----------	6.01
50-chloride	----------	168	----------	----------	----------	5.99
150-chloride	----------	347	----------	----------	----------	5.66
50-sulfate	----------	----------	89	----------	----------	6.00
150-sulfate	----------	----------	96	----------	----------	6.02
250-sulfate	----------	----------	91	----------	----------	6.02

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[1] First cutting.

The method used for sap extraction does not permit of any orientation of the findings with respect to the more detailed loci of accumulation. It seems safe to conclude, nevertheless, that salt accumulation extended both to the vacuolar and the cytoplasmic fluids, and accompanying the resulting equilibrium between these, the bases particularly may have become important constituents of the cell-wall materials bringing about structural changes or differences in extensibility. These questions must wait upon further investigations, as must questions that have to do with the influence of these inorganic additions to the sap upon the elaboration, destruction, or action of plant hormones, or upon carbon assimilation and photosynthesis.

The reduction in pH values associated with chloride accumulation in the expressed sap must also for the time be regarded as having an uncertain significance. A suggestion that importance may be attached to the change in pH values accompanying chloride accumulation is afforded by the fact that sugar beets accumulated chloride without change in hydrogen-ion concentration., and this plant was the only one measured which was not injured significantly by additions of 150 milliequivalents to the nutrient solution. Van Itallic (34), observing a decrease in the pH values of tissues of potatoes grown on soils to which sodium chloride was added, concluded that this was the cause of chloride injury rather than the chloride itself. He thought that the pH values were reduced because the plant took up more chloride than sodium. Without questioning the importance of the buffer system of the plant and the dependence of normal activity on the maintenance of characteristic hydrogen-ion concentrations, it is nevertheless appropriate to leave open for further investigation the significance of change in the hydrogen-ion concentration and its meaning in terms of salt injury. Furthermore, it is to be remembered that sulfate salts were likewise toxic and that large quantities of sulfur were found in the expressed saps and yet there was no associated change in the hydrogen-ion concentration.

Masacwa (21), working principally with buckwheat, advanced the idea that the physiological basis of injury is not the chloride itself but rather the fact that the excess chloride was taken up with calcium and that the normal K/Ca balance was thereby upset. With the plants of the present experiments it might be difficult to substantiate a conclusion that potassium was deficient or that the K/Ca ratios were unfavorable to growth. Along wholly different lines, Baslavskaja (2) reported lower chlorophyll content of potatoes and also higher water content in the leaves of both tobacco and potatoes as a result of the addition of chloride. In potato leaves, a reduction in total carbohydrates (3) was associated with a reduction in chlorophyll.

EFFECT OF CHLORIDE AND SULFATE SALTS ON CORN, TOMATOES, AND WHEAT IN GREENHOUSE WATER-CULTURE EXPERIMENTS

Experiments in the greenhouse on corn, tomatoes, and wheat in water culture had three principal objectives, namely, to determine (1) whether the high toxicity of chloride and sulfate salts noted in the outdoor sand-culture experiments was in some way peculiar to the experimental methods employed, (2) the effects on growth of relatively low concentrations of chloride and sulfate salt's, and (3) the character of the growth-depression curves through low as well as high concentrations of these salts. For this reexamination of the problem wholly different methods were employed. A series of five water-culture experiments were conducted in the greenhouse; corn and tomatoes were used as test plants in both chloride and sulfate experiments; and finally there was an experiment with wheat in sodium chloride solutions.

METHODS AND MATERIALS

Though the aeration of water cultures is regarded as highly desirable, facilities could not be arranged for aerating the large number of small cultures essential for the purposes of the tests. To provide for some exchange of gas between the solution and the outside atmosphere, special covers were built for the quart mason jars used as culture vessels, Pieces of ¼-inch galvanized screen wire were cut in disks of such size that they would be held in place on top of the wide-mouth jars by the standard open-center screw rings such as are used for canning. An upright collar of galvanized iron, 1.5 inches tall, was soldered to the screen wire (see figs. 5 and 7). After the selected seedlings from the germination trays had been placed on the screen, with their roots in the culture solution, beach pebbles were filled in around the stems to hold the plants upright. Thin paper squares slipped around the stems kept the tomato seedlings from sliding through the meshes of the screens.

The lighting conditions in the greenhouse in which the experiments were conducted were not very uniform. To provide uniform conditions for all cultures of a test, the jars were arranged in a single row near the outer edge of a clinostat the diameter of which was 6.2 feet. The circumference of the clinostat limited the number of cultures to about 50. The table made 1 revolution in 4 minutes.

The corn plants were the F_1 generation of a hybrid between two strains of a soft American Indian type known as Sacaton June. The parents of this seed[5] had each been selfed through six generations. Stone tomatoes and Baart wheat were used as the other test plants. All of the seeds were germinated on cotton netting over tap water (15) and, as soon as the roots were sufficiently developed to permit, transferred to the culture solutions. The cultures were left in the laboratory for 24 hours before they were placed in the lighted greenhouse.

The ionic concentrations of the base nutrient solutions used for these tests are shown in table 12. In the same table are shown the

TABLE 12.—Composition of *the base nutrient solutions used in the water culture greenhouse experiments reported in tables 14 to 18*

Crop and ion	Constituent of base nutrient (milliequivalents per liter)									Chloride and sulfate salts added (percent, as milliequivalents, of)—		
	Ca	Mg	Na	K	NH_4	NO_3	H_2PO_4	SO_4	Cl	Ca	Mg	Na
Corn (chloride)	8	4	------	4.25	4	12	0.25	8	------	25	25	50
Corn (sulfate)	8	4	------	4.25	4	12	.25	1	7	15	35	50
Tomato (chloride)	8	4	------	4.50	4	12	.50	8	------	25	25	50
Tomato (sulfate)	8	5	4	4.50	2	12	.50	1	10	15	35	50
Wheat (chloride)	14.5	3.6	------	7.20	------	17.7	4.00	3.6	------	------	------	100

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[5] Supplied by J. H. Kempton and the late G. N. Collins, of the Bureau of Plant Industry, U. S. Department of Agriculture.

proportions of calcium, magnesium, and sodium salts used in the introduction of the additional chloride and sulfate. In the four experiments with corn and tomatoes, 50 percent of the chloride and sulfate was introduced as the sodium salt. The remaining 50 percent was added as calcium and magnesium salts. The culture solutions were prepared from chemicals of reagent or equal quality. There was also added to the solutions 1 p. p. m. of boron, 0.1 p. p. m. of zinc, and 0.1 p. p. m. of manganese, and, in very small amounts, a mixture of 28 additional elements. Iron citrate was added to the newly prepared solutions to give a concentration of 5 p. p. m. of iron, and more was added occasionally thereafter as required. In the experiment with wheat, which was designed to parallel the experiments of Lipman, Davis, and West (*17*), chloride was added as the sodium salt and the base nutrient solution contained the same proportions of nutritive ions that they used. The concentrations of the chloride and sulfate employed in the successive experiments are shown in conjunction with the results reported in tables 14 to 18. Dates, duration of the experiments, and changes of solutions are recorded in table 13.

TABLE 13.—*Duration of and changes of nutrient solutions in the water-culture greenhouse experiments reported in tables 14 to 18*

Crop and ion	Test started	Test ended	Duration	Period from start to change of nutrient solution			
	1936	*1936*	*Days*	*Days*	*Days*	*Days*	*Days*
Corn (chloride)	Apr. 4	May 2	28	12	21	26	--------
Corn (sulfate)	June 25	July 21	26	14	20	--------	--------
Tomato (chloride)	Oct. 16	Nov. 20	35	14	20	--------	--------
	1937	*1937*					
Tomato (sulfate)	Jan. 8	Feb. 19	42	5	25	32	38
Wheat (sodium chloride)	Mar. 21	May 10	50	44	--------	--------	--------

Transpiration data were obtained by measuring the volume of water added to the cultures to replace that taken up by the plants. A check jar without plants was carried through each experiment, and the evaporation from it was deducted from the total water loss from each of the cultures.

It should be pointed out that the results of the five experiments are not wholly comparable with one another, in terms of the degree of salt toxicity or the relative toxicity of chloride and sulfate salts, because of the differences in the greenhouse temperatures, day lengths, and other factors related to the season of the year in which the successive experiments were conducted, as well as differences in maturity of the plants and the composition of the base nutrient solutions.

CORN IN CHLORIDE SOLUTIONS (EXPERIMENT 3)

As shown in table 14 and figure 4, the growth of corn in this experiment was depressed by relatively low concentrations of chloride. Just where injury first occurred is difficult to determine, because of the reaction of 2 of the 12 plants in 8 milliequivalents of chloride; these 2 plants had green weights of 19.8 and 24.5 gm., whereas the average of the weights of the 8 plants in the other 2 jars of the treatment was 12.7 gm., suggesting that the 2 plants were in some way different and that there would be justification for disregarding either this

TABLE 14.—*Effect of chloride salts on growth of corn in water cultures (experiment 3)*

Chloride concentration (m. e./l.)	Jars	Plants	Average green weight of tops per plant	Standard error	Average dry weight of tops per plant	Average dry weight of entire plants	Moisture in green tops	Roots [1]	Water requirement [2]
	Number	*Number*	*Grams*	*Grams*	*Grams*	*Grams*	*Percent*	*Percent*	*Grams*
[3]	10	40	14.8	0.41	1.13	1.54	92	26.9	254
2	10	40	14.9	.38	1.11	1.55	93	28.4	246
4	3	12	14.7	.47	1.08	1.54	93	29.6	242
6	3	12	13.8	.71	1.01	1.41	93	28.4	252
8	3	12	15.0	1.08	1.10	1.52	93	27.4	256
10	3	12	12.7	.55	.92	1.28	93	27.9	259
15	3	12	12.3	.64	.92	1.28	93	28.2	264
20	3	12	11.1	.92	.81	1.15	93	29.7	268
35	3	12	9.9	.44	.79	1.16	92	32.3	236
50	3	12	9.4	.74	.78	1.22	92	35.8	222
75	3	12	6.5	.52	.53	.88	92	39.4	244
100	3	12	6.4	.44	.58	.96	91	41.1	179

[1] Measured as percentage of entire plants.
[2] Measured as grams of water per gram of dry material.
[3] Trace.

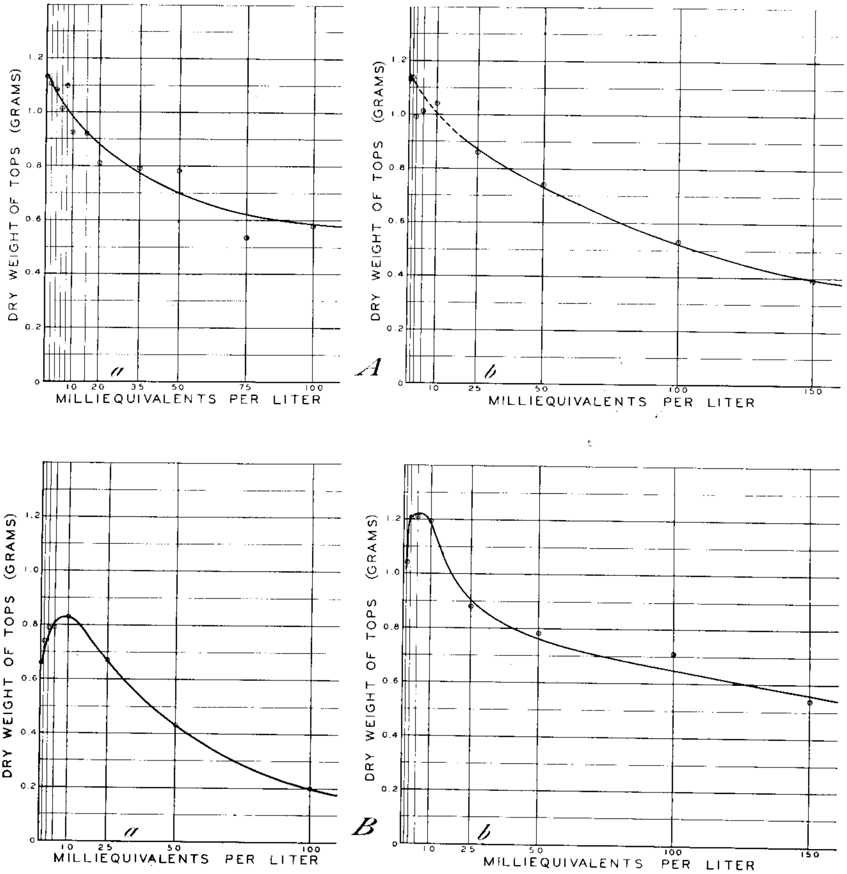

FIGURE 4.—Depression in growth of plants in greenhouse water-culture experiments; *A*, Corn with chloride (*a*) and sulfate (*b*) salts; *B*, tomatoes with chloride (*a*) and sulfate (*b*) salts. (Experiments 3, 4, 5, 6, respectively.)

jar or the entire treatment. If this is done, a decreasing growth trend follows from the lowest to the highest concentrations.

There was little effect of the treatments on the moisture content of the plants other than that associated with the burning of the tips of leaves in the higher concentrations. In these higher concentrations the weight of roots relative to the weight of tops increased and the water-requirement values decreased.

The toxicity of chloride per unit of salt added being greater over the range from 4 to 20 milliequivalents than from 20 to 100, the growth-depression curve (fig. 4) tended to flatten with increasing concentrations of salts.

CORN IN SULFATE SOLUTIONS (EXPERIMENT 4)

A sulfate concentration of 1 milliequivalent per liter resulted in slightly larger plants than 2.5 milliequivalents, indicating that under the conditions of experiment 4 the sulfate requirements of corn were relatively low (table 15). As in the preceding test with corn, there were decreasing moisture percentages in the green plants as the amount of tip burning increased. The weight of roots relative to entire plants increased, and the water requirements decreased through the higher sulfate concentrations. These relations being the same as in the preceding experiment with corn in chloride solutions, the effect cannot be regarded as peculiar to either of these anions. The growth-depression curve (fig. 4, A, *b*) resembles that for corn in chloride (fig. 4, A, a).

TABLE 15.—*Effect of sulfate salts on growth of corn in water cultures (experiment 4)*

Sulfate concentration (m. e./l.)	Jars	Plants	Average green weight of tops per plant	Standard error	Average dry weight of tops per plant	Average dry weight of entire plants	Moisture in green tops	Roots[1]	Water requirement[2]
	Number	*Number*	*Grams*	*Gram*	Grams	*Grams*	*Percent*	*Percent*	*Grams*
1	6	24	13.0	0.73	1.13	1.51	91	25.0	414
2.5	6	24	10.7	.56	.99	1.33	91	25.4	416
5	6	24	11.0	.66	1.01	1.34	91	24.9	420
10	6	24	11.9	.78	1.04	1.38	91	24.3	418
25	6	24	8.8	.40	.86	1.20	90	28.1	401
50	6	24	7.6	.46	.74	1.05	90	29.2	370
100	6	24	4.0	.40	.53	.82	87	35.0	289
150	6	24	2.3	.27	.39	.62	83	36.8	228

[1] Measured as percentage of entire plants.
[2] Measured as grams of water per gram of dry material.

TOMATOES IN CHLORIDE SOLUTIONS (EXPERIMENT 5)

Evidence of a substantial benefit to tomatoes from chloride concentration as high as 10 milliequivalents per liter resulted from experiment 5 (table 16). This evidence of a beneficial effect of chloride ion on tomatoes finds confirmation in a subsequent experiment reported in this paper (p. 388). No deficiency symptoms could be observed at concentrations below 10 milliequivalents nor did the leaves of the plants burn or show other symptoms of diagnostic value at the high chloride concentrations.

Chloride was without effect on the moisture content of the green tops. The lowest percentage of roots was found in the range of concentrations that produced the greatest weight of entire plants. The water-requirement values decreased through the series of concentrations. Analysis of the leaves of these tomatoes, grown in unaerated water cultures, showed relatively more chloride than was found in tomato leaves from the outdoor sand-culture experiment.

TABLE 16.—*Effect of chloride salts on growth of tomatoes in water cultures (experiment 5)*

Chloride concentration (m. e./l.)	Jars	Plants	Average green weight of tops per plant	Standard error	Average dry weight of tops per plant	Average dry weight of entire plants	Moisture in green tops	Roots [1]	Water requirement [2]
	Number	*Number*	*Grams*	*Gram*	*Gram*	*Grams*	*Percent*	*Percent*	*Grams*
(3)	6	18	9. 1	0. 28	0. 66	0. 88	93	24. 1	562
1	6	18	11. 4	. 36	. 74	. 95	94	21. 6	537
2.5	6	18	12. 1	. 42	. 79	1. 01	93	21. 6	524
5	6	18	12. 7	. 44	. 79	. 98	94	18. 7	540
10	6	18	13. 6	. 49	. 83	1. 03	94	20. 7	527
25	6	18	10. 6	. 55	. 67	. 86	94	22. 6	479
50	6	18	6. 5	. 40	. 43	. 57	93	24. 5	452
100	6	18	3. 0	. 19	. 20	. 29	93	31. 2	437

[1] Measured as percentage of entire plants.
[2] Measured as grams of water per gram of dry material.
[3] Trace.

TOMATOES IN SULFATE SOLUTIONS (EXPERIMENT 6)

In sulfate concentrations of 2.5, 5.0, and 10 milliequivalents the tomato plants were of approximately equal weight. Growth was slightly depressed in the solutions with only 1 milliequivalent of sulfate, and in solutions with more than 10 milliequivalents of sulfate successive reductions in growth occurred. The moisture content of the plants decreased slightly and the water-requirement values decreased considerably as the concentration of sulfate was increased (table 17). Symptoms of injury other than decrease in size were not in evidence. Cultures from this experiment are shown in figure 5.

TABLE 17.—*Effect of sulfate salts on growth of tomatoes in water cultures (experiment 6)*

Sulfate concentration (m. e./l)	Jars	Plants	Average green weight of tops per plant	Standard error	Average dry weight of tops per plant	Average dry weight of entire plants	Moisture in green tops	Roots [1]	Water requirement [2]
	Number	*Number*	*Grams*	*Grams*	*Grams*	*Grams*	*Percent*	*Percent*	*Grams*
1	6	18	16. 2	0. 65	1. 04	1. 27	94	18. 2	524
2.5	6	18	19. 5	1. 05	1. 21	1. 45	94	16. 4	514
5	6	18	19. 6	1. 03	1. 21	1. 43	94	15. 5	519
10	6	18	18. 4	. 97	1. 19	1. 44	94	17. 6	494
25	6	18	12. 7	. 96	. 88	1. 08	93	19. 0	497
50	6	18	10. 8	. 67	. 78	. 99	93	20. 7	449
100	6	18	9. 2	. 66	. 71	. 88	92	19. 0	388
150	6	18	6. 3	. 29	. 54	. 67	91	20. 1	365

[1] Measured as percentage of entire plants.
[2] Measured as grams of water per gram of dry material.

WHEAT IN SODIUM CHLORIDE SOLUTIONS (EXPERIMENT 7)

In the experiment with wheat grown in chloride solutions, boron, manganese, and zinc, together with a very small amount of a mixture of 28 additional elements, were added to four of the eight cultures of

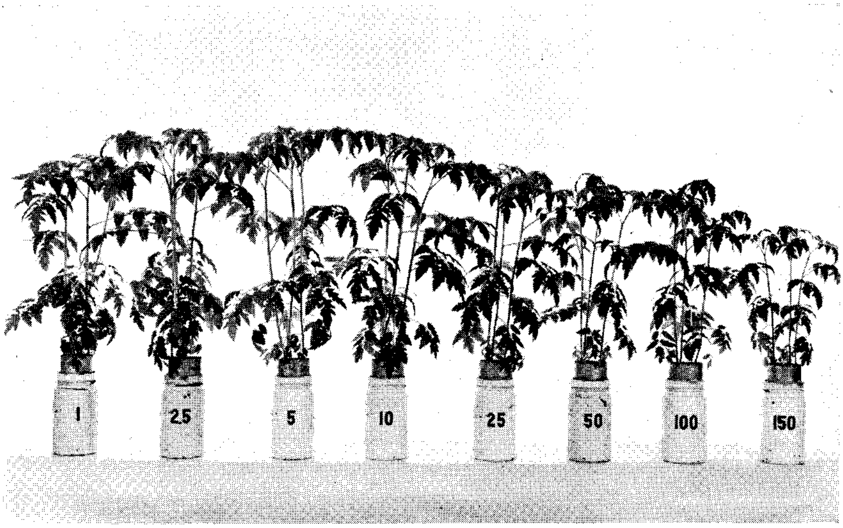

FIGURE 5.—Cultures of tomatoes grown in solutions with sulfate. Figures on jars show concentrations of sulfate ion in milliequivalents per liter. (Experiment 6.)

each treatment and omitted from the other four. The plants that received the added elements made only slightly better growth than those that did not (table 18). The graphs (fig. 6) of the two sets of plants are otherwise similar. Both indicate that 10 milliequivalents

TABLE 18.—*Effect of sodium chloride on growth of wheat in water cultures (experiment 7)*

[Intended to reproduce an experiment by Lipman, Davis, and West (*17*)]

WITH TRACE ELEMENTS B, MN, ZN, AND 28 OTHERS

NaCl concentration (m. e./l.)	Green weight of 6 plants per jar					Average dry weight of entire plants per jar	Moisture in entire green plants	Roots [1]	Water requirement [2]
	Jar 1	Jar 2	Jar 3	Jar 4	Average				
	Grams	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Percent*	*Percent*	*Grams*
(3)	71	75	72	66	71.0	7.48	89	21.1	648
10	66	69	77	81	73.3	7.23	90	23.2	702
50	34	42	40	36	38.0	4.80	87	28.1	612
100	14	8	12	18	13.0	2.05	84	18.2	525
200	----	----	----	----	----	[4].47	----	----	545
300	----	----	----	----	----	(5)	----	----	----

WITHOUT TRACE ELEMENTS

NaCl concentration (m. e./l.)	Jar 1	Jar 2	Jar 3	Jar 4	Average	Average dry weight of entire plants per jar	Moisture in entire green plants	Roots [1]	Water requirement [2]
(3)	71	75	74	58	69.5	7.10	90	21.4	699
10	76	72	62	64	68.5	6.73	90	23.4	694
50	34	39	30	33	34.0	4.37	87	25.3	651
100	10	12	12	12	11.5	1.93	83	19.4	557
200	----	----	----	----	----	[6].43	----	----	570
300	----	----	----	----	----	(5)	----	----	----

[1] Measured as percentage of entire plants.
[2] Measured as grams of water per gram of dry material.
[3] Trace.
[4] Only 2 plants survived.
[5] All plants died at an early stage.
[6] Only 3 plants survived.

of sodium chloride was slightly toxic and 50 and 100 milliequivalents decidedly so. Plants in 200 milliequivalents made little growth.

The methods employed in this test were not different in essential details from those employed by Lipman, Davis, and West (*17*) in their work with wheat in sodium chloride solutions. They found that depressed growth resulted only when the concentration of chloride was increased to 90 milliequivalents per liter. In their work, conducted as it was in the years 1920 to 1922, elements such as boron, manganese, and zinc were not added to the solutions except when introduced as impurities. The present experiment does not provide an explanation of the differences in the two sets of results. It is possible, however, that their base nutrient salts were exceptionally free from trace elements and that these elements were introduced with the sodium chloride in amounts just sufficient through the successive concentrations up to 90 milliequivalents to offset salt toxicity.

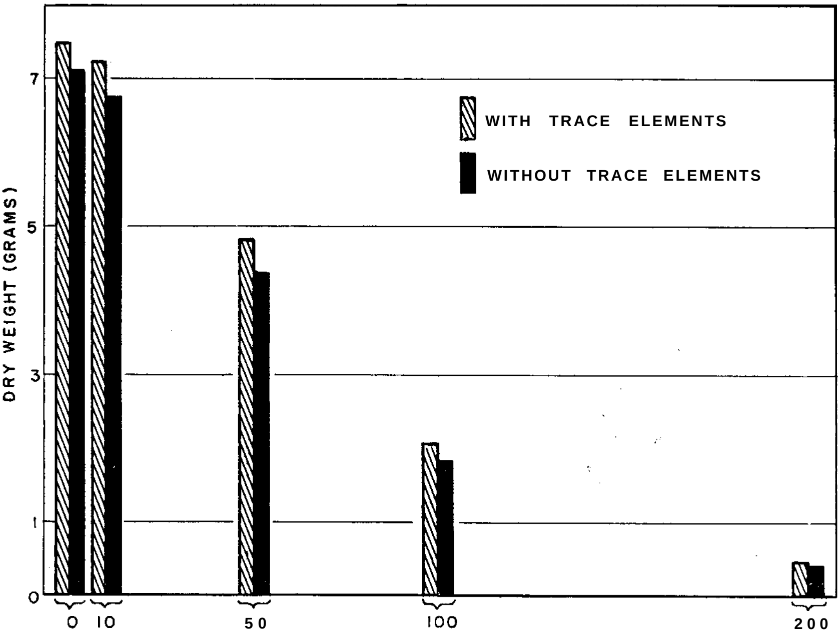

FIGURE 6.—Effect of sodium chloride on growth of wheat with and without the addition of trace elements.

The moisture content of the green plants (table IS) decreased with increased burning. Water requirements were reduced with the addition of salt as in the preceding experiments with corn and cotton and as in the Lipman, Davis, and West (17) experiments. It may be observed (fig. 7), that 10 milliequivalents of chloride tended to increase the height but not the weight of wheat plants.

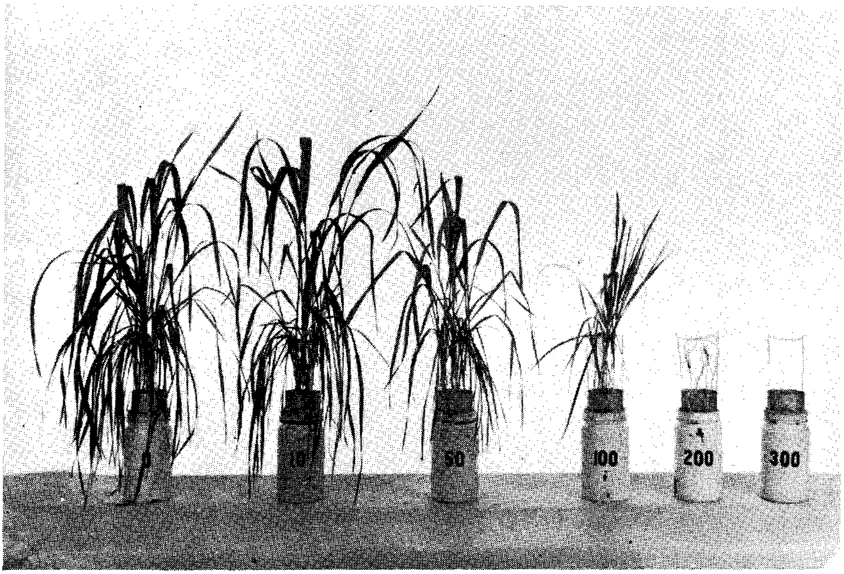

FIGURE 7.-Wheat grown in solutions with sodium chloride. Numbers on jars show concentrations of sodium chloride in milliequivalents per liter. (Experiment 7.)

BENEFICIAL EFFECT OF CHLORIDE ON THE EARLY GROWTH OF TOMATO AND COTTON PLANTS (EXPERIMENT 8)

Following the observation of the beneficial effects of a small quantity of chloride ion on tomatoes grown in tho water-culture tests, two somewhat incidental experiments were conducted in sand cultures in the greenhouse for the purpose of further observation.

Tomatoes were grown in 27 sand cultures supplied with only the trace of chloride originating as an impurity in the sand and nutrient solution and in 27 otherwise similar cultures maintained with a nutrient solution containing 3 milliequivalents of chloride. After the tomato plants had been cropped the experiment was repeated with cotton Both experiments are reported in table 19. The base nutrient solution used for the tomatoes contained, in addition to the trace elements boron, manganese, and zinc, 4 millimoles each of calcium nitrate ($Ca (NO,),$) and potassium nitrate (KNO_3), 2 millimolcs per liter each of magnesium sulfate ($MgSO_4$) and ammonium sulfate ($(NH_4)_2SO_4$), and I millimolc of monopotassium phosphate (KH_2PO_4). In the cotton test 0.5 millimolc of sodium sulfate (Na_2SO_4) was added to the above solution, and half of the ammonium sulfate was omitted. The chloride ion was supplied as sodium chloride ($NaCl$).

The culture vessels were 2-quart Oldberg-type percolator tubes. These were fitted with a wad of glass wool above the tubular opening at the base and filled to within about 3 inches of the top with quartz sand. Two l-quart mason jars were used in conjunction with each. One of these, placed beneath the tubes, collected percolate when nutrient solution was applied from the other. After the daily or more frequent passage of the nutrient solution through the sand it was returned to volume with distilled water, and the positions of the two jars were reversed.

Eighteen of the percolator tubes were suspended through openings near the rim of each of three clinostats. These clinostats, which were 4.5 feet in diameter, were set flush with a 15-foot greenhouse bench and formed rotating disks in the top of it. The collecting jars rested at an appropriate height on circular shelves suspended from the tops of the rotating clinostats. The three clinostats were driven by a single endless belt.

In each culture the tomato plants were grown from July 27 to September 22, 1936, and the cotton plants from January 2 to March 10, 19x7.

Both tomatoes and cotton responded to the addition of 3 milliequivalents of chloride. On the basis of clinostats A, B, and C, taken collectively, the growth of tomatoes as measured by green weight was greater by 35 percent, and the growth of cotton as measured by green weight was greater by 81 percent, when supplied with 3 milliequivalents of chloride than when only a trace was present (table 19).

TABLE 19.—*Effect of 3 milliequivalents of chloride on growth of tomatoes and cotton in sand cultures in the greenhouse (experiment 8)*

Crop plant and treatment	Clinostat	Cultures	Plants	Average green weight per plant	Standard error
Tomatoes:		*Number*	*Number*	*Grams*	*Grams*
Trace of chloride	A	9	27	18.6	1.02
	B	9	27	14.9	.75
	C	9	27	15.9	.57
Total or average		27	81	16.5	4 9
3 milliequivalents of chloride	A	9	27	25. A	.95
	B	9	27	23.0	1.03
	C	9	27	18.1	.81
Total or average		27	81	22.2	64
Cotton:					
Trace of chloride	A	9	27	10.5	1.20
	B	9	27	11.7	1.41
	C	9	27	14.2	1.17
Total or average		27	81	12.1	.78
3 milliequivalents of chloride	A	9	27	28.1	1.91
	B	9	27	20.8	1.03
	C	9	27	16.7	1.21
Total or average		27	81	21.9	1.21

The differences in the growth of the similarly treated plants on the three adjacent clinostats is probably typical of what takes place in many small greenhouses. The distance between the centers of adjacent clinostats was less than 5 feet, and they were rotated continuously both night and day. The center line of the clinostat assembly was parallel with and 5.5 feet away from the south face of the greenhouse.

In the following discussion, references are made to the extensive literature that exists on the effects of relatively small amounts of chloride on the growth of plants. The results reported in tables 14 and 17 seem especially noteworthy in that in most of the earlier work much lower concentrations were customarily used and rarely have responses as great as these been obtained.

GENERAL DISCUSSION

All irrigation waters, whether diverted from streams or pumped from underground aquifers, carry salts in solution. These salt's are variously derived from the rock and alluvial materials with which the waters have been in contact, from the residues of past or present lakes, marshes, inland seas, and estuaries, and from the drainage of upstream or overlying irrigated lands and the seepage from subirrigated areas supporting vegetation along watercourses. By reason of evaporation from soil surfaces, the uptake of water in excess of salts by plants, and the rise of salt from saline subsoils and water tables, it is quite regularly found that the soil solutions are more saline than the irrigation supply. Depending upon the extent of root-zone leaching and the removal of the percolate by drainage, the accumulation of salt in soils may be of nominal magnitude, or concentration may increase to such a degree that agricultural operations become unprofitable. The salt constituents of irrigation water may affect plant growth adversely owing to their excessive accumulation in the soil and later in the plants or to changes in the physical and chemical characteristics of soils that impede water penetration or otherwise cause the soil environment to be less favorable as a medium for root development.

Whatever the source or kind of salt, the extent of its accumulation, or the mechanism of its ill effects, salinity is apt to be an important factor in irrigation agriculture wherever it is practiced. In the discussion that follows, features of the salinity problem are briefly touched upon that have seemed to the writer to merit consideration not only from the standpoint of the data that have preceded but in a broader way from that of plant and salt relations under conditions of irrigation agriculture.

The absence of leaf symptoms or other pronounced outward abnormalities in a number of plants whose growth was depressed by salt has been noted in this paper. Before undertaking the present experiments the author had come to regard this feature of the salt relations of plants as one of special interest. Both in the field and in. minor experiments, where comparisons were possible between plants growing on saline and those growing on nonsaline soils, it had been observed that many salt-injured plants developed no symptoms of diagnostic significance. These observations suggested that a substantial proportion of the curtailed production of crops in irrigated areas that was attributed to nutritional deficiencies or unfavorable water relations was in fact due to saline conditions customarily regarded as insufficiently high to be a cause of reduced yields.

In the absence of symptoms of injury and without an opportunity for direct growth comparisons with plants on adjacent nonsaline soils, the drawing of significant conclusions on salt injury under field conditions must be regarded as difficult. Loughridge (19, *p.39*), for example, published a table under the heading "Highest amount of alkali in which fruit trees, other trees, and small cultures were found unaffected." This table, which has been reprinted in one of the important soil-reference books (*14*), has had an extensive influence, and yet it is based entirely upon the appearance of plants in the field as judged by its author.

The two 13-year-old grapefruit orchards shown in figures 8 and 9 are illustrative of the foregoing situation as it is encountered when

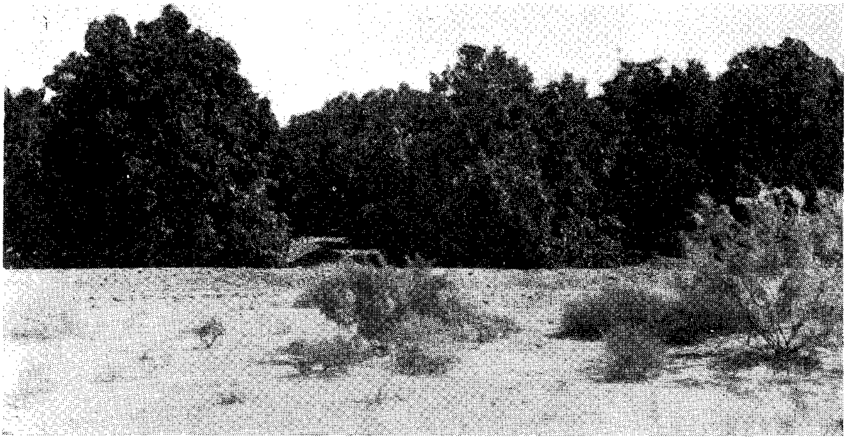

FIGURE 8.—Thirteen-year-old grapefruit grove on Superstition sand, Yuma Mesa, Ariz.; irrigated with Colorado River water. The yield in 1936 was 546 pounds of fruit per tree. The character of this soil and the irrigation practice have been such that there has been little accumulation of salt in the root zone, i. e., the water has been applied substantially in excess of evaporation and transpiration losses. The grove is vigorous and the trees large. Analyses of displaced soil solutions and of the irrigation water are shown in table 20.

one endeavors to interpret the significance of salt concentrations found in field soils. Both of these orchards were on deep alluvial soils and both were irrigated from the same water supply. The poor orchard on the relatively impermeable saline soil (fig. 9), notwithstanding the contrast with the good orchard (fig. 8), appeared reasonably healthy

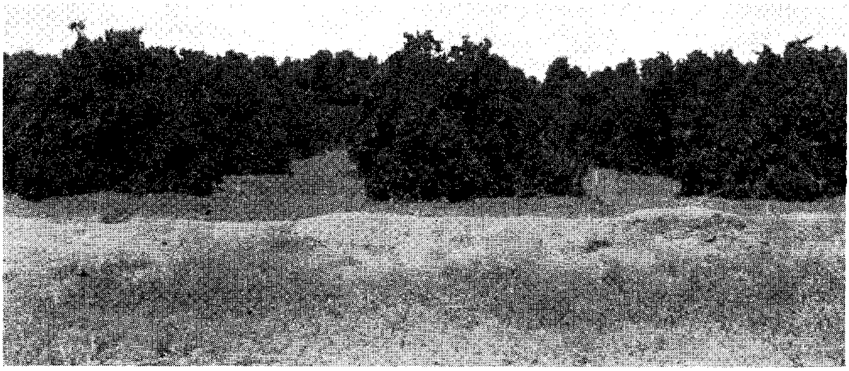

FIGURE 9.—Thirteen-year-old grapefruit grove on Holtville silty clay, Meloland, Imperial Valley, Calif.; irrigated with Colorado River water. The yield is less than 100 pounds of fruit per tree. The character of the soil in this orchard is such that it apparently has not been possible to leach the salt residues of the irrigation water beyond the root zone. The trees have good color and are heavily foliated. There are few yellow or burned leaves. The trees and individual leaves are smaller than those of the trees shown in figure 8, but salt-injury symptoms of diagnostic value are otherwise lacking. Analyses of displaced soil solutions and of the irrigation water are shown in table 20.

and the foliage was of good color, but the yield was low. Several years later, when the poor orchard was again visited, deadwood was observed in the tops of some of the trees, the leaves were small and many were yellowed to varying degrees, with some burning of the leaf tips.

Not a little of the difficulty that has attended the interpretation of the analyses of field soils in terms of plant reactions has been due to the common practice of referencing the quantity of salt found to the dry weight of the soil instead of stating the concentration as of the soil solution. The critical nature of this consideration can be illustrated by assuming two soils--one with a moisture equivalent or field-carrying capacity of 4 percent and the other of 40 percent. Should each of these soils contain 500 p. p. m., or 0.05 percent, of chloride on dry-weight basis, then the soil-solution concentration at the moisture equivalent in the first soil would be 12,500 p. p.m. and in the second soil 1,250 p. p. m. A creditable growth of a crop like milo could be expected on the latter soil, but on the first few if any agricultural plants would survive. The analyses of the soil solution reported in table 20 are useful as a further illustration. In terms of soil solutions, the concentration of chloride found in the fourth foot of the poor orchard (fig. 9) is 9.5 times as high as that in the fourth foot of the good orchard. Had these same quantities of chloride been recorded in terms of the dry weight of soil, the concentration in the poor orchard would have been 95.6 times that in the good orchard.

TABLE 20.—*Analyses of displaced soil solutions of Superstition sand and Holtville silty clay, from grapefruit groves in Arizona and California, and of the irrigation water from the Colorado River as sampled at Yuma, Ariz.*

[Analyses of displaced soil solutions are adjusted to the moisture equivalent]

Origin and depth of sample	Moisture equivalent	pH	Conductance (K × 10^5 at 25° C.)	Boron	Other constituents (milliequivalents per liter)							
					Ca	Mg	Na	K	HCO_3	SO_4	Cl	NO_3
Superstition sand:[1]				*P. p. m*								
First foot	11.4	7.4	219	0.84	6.48	6.58	9.51	0.72	5.40	7.65	11.51	0.72
Second foot	3.4	6.4	226	.44	8.71	4.47	9.62	.80	3.89	9.62	8.66	.98
Third foot	4.6	6.7	200	.38	7.37	3.83	8.83	.60	3.25	9.11	7.24	.87
Fourth foot	5.4	7.0	210	.36	7.75	4.20	9.42	.53	2.10	11.27	7.25	.90
Fifth foot	3.8	6.6	240	.59	8.18	4.73	11.06	.66	2.29	14.24	7.82	1.19
Sixth foot	3.9	6.6	320	.48	11.79	6.62	14.49	.92	1.75	19.43	12.21	1.22
Holtville silty clay:[2]												
First foot	22.7	7.7	685	1.05	24.46	21.57	38.31	.95	4.07	54.37	27.15	.54
Second foot	18.1	7.7	1,087	1.03	37.40	28.57	69.10	.85	4.26	75.69	54.03	1.09
Third foot	25.9	7.4	1,480	.75	38.59	39.86	99.70	.22	1.99	54.37	119.32	.45
Fourth foot	45.7	7.3	1,229	.87	33.39	34.07	78.92	.15	1.51	39.81	106.75	.40
Fifth foot	45.3	7.0	1,092	1.25	26.33	28.37	76.18	.08	.90	47.96	85.21	.45
Sixth foot	37.4	7.6	769	.79	18.69	18.14	54.87	(3)	.85	48.68	45.65	.37
Colorado River[4]	--------		137	.17	5.41	3.01	6.47		3.19	7.71	3.68	.11

[1] Soil samples collected June 30, 1936. [2] Soil samples collected July 1, 1936. [3] Trace.

[4] Eight-year, unweighted weekly average (Oct. 1, 1928, to Sept. 30, 1936).

Inasmuch as the reaction of plants to salt constituents of the soil is dependent upon the concentration of the solution, there is obvious need for investigators to agree upon the most suitable moisture condition of the soil to be taken as a base. The moisture equivalent corresponds approximately to a constant value of the capillary potential or soil-moisture tension for different soils. With this base it is at once apparent that concentrations will tend to double as the wilting coefficient of the soil is approached. Breazcalc (*4*) has suggested referencing salt concentrations to the moisture content of soils at the wilting coefficient. However, the moisture equivalent of soils, which corresponds roughly in well-drained soils to field capacity, is more easily ascertained than the wilting coefficient, and where displacement methods arc employed the soils are customarily wet to the moisture equivalent.

Plants have been grown extensively in undrained potted soils in which known amounts of salt were incorporated by careful mixing. Water applied to the surface of the soils to maintain the plants would unavoidably wash the salts downward, leaving the upper and better aerated zones relatively free from salt. In one investigation (*24*, *25*), where 4-gallon stone jars were used in this manner, it was found that additions of sodium carbonate and sodium chloride as high as 0.4 percent of the dry weight of the soil and sodium sulfate as high as 0.9 percent were as often stimulating as toxic. This type of finding is not in accord with the results reported in this paper.

The water-holding capacity of suspended soils, that is, soils in containers 1 or 2 feet deep, even when provided with drainage, may exceed that of the same soil in the field two or three times, giving rise to the possibility of conditions of poor aeration such as exist in waterlogged lands. The conditions in poorly aerated soils are those conducive to the reduction of sulfate and nitrate into more toxic forms.

Experiments conducted with culture solutions may lead to erroneous conclusions if special care is not employed to maintain the concentrations of nutrient ions in the control cultures at levels as high as those in the salt cultures. The significance of this consideration was once brought out in an experiment with cotton plants grown in automatically flushed greenhouse sand cultures. Because of the pressure of other work, the writer was unable to change the nutrient solutions in the reservoirs as soon as planned; this being the case, it seemed best to give up the original purpose for which the plants were being grown and continue to care for them without further change of the solutions. At the time the solutions should have been replaced, the control plants were far ahead of the chloride and sulfate plants. The growth rate of the control plants soon declined, whereas that of the chloride and sulfate plants was maintained for a time, with the result that by the end of the fourth week there was little difference either in general appearance or size of the three lots. This experiment would seem to indicate that a plant such as cotton, with an indeterminate growth habit, can utilize a like supply of nutrients from a saline substrate about as effectively as a more rapidly growing plant on a nonsaline substrate, but it requires more time to do it.

It is not unlikely that conditions such as those outlined in the preceding paragraph may sometimes lead to the production of as high yields on saline soils of limited fertility as are obtained on otherwise similar nonsaline soils. In recognizing this as a possibility, however, account should be taken of the fact that salt concentrations typically, though not universally, increase with depth, as was illustrated in table 20. Experiments that can only be touched upon here have shown that, when the roots of a plant are divided between two vessels, the part of the root system in a concentrated solution does not develop as rapidly as the part in a dilute solution. In other words, to apply the foregoing observation to the field, it seems necessary to recognize that the roots of the slow-growing crop on saline soil might never fully occupy the deeper and more saline portion of the soil and, failing in this respect, its total supply of nutrients would not be equal to that available to the crop on the nonsaline soil.

It has come to be generally recognized that with the introduction of salts, particularly sodium salts, into soils there may be marked effects upon the availability of nutritive ions. Effects of this kind on the growth of plants are apt to be outstanding in pot experiments since, in such case, the soil volume relative to the number of plants is customarily small and any increase in the availability of nutritive ions is commonly reflected by substantial increase in growth. Potassium released by base exchange processes usually receives the primary consideration in this connection, but the indirect effects are not necessarily limited to this ion. Sokoloff (*31*), for example, has found higher nitrate concentrations in soils treated with sodium salts than in soils treated with calcium salts. The increases in soluble nitrogen were accompanied by the evolution of carbon dioxide, and the effect is attributed by Sokoloff to a more rapid biological oxidation of the nitrogen of humus. It has been found by experiments not included in this report that better growth resulted on a low-nitrogen soil when sodium chloride was added than when calcium chloride was added; whereas with the addition of nitrogen the reverse was observed. Without the addition of nitrogen, the sodium treatment increased the growth of tomatoes and barley above that of the control plants; smaller increases were shown by cotton plants.

In some instances nitrate accumulation has been found to accompany chloride and sulfate accumulation in irrigated soils, and, if the concentration is not excessive, the productivity of the land may thereby be increased; but it does not follow that there is any substantial reduction in the toxicity of chloride or of sulfate if comparisons are made between saline and nonsaline soils at equal nitrate levels. In an experiment conducted during the winter and spring months in the outdoor sand beds, onions, alfalfa, barley, and table beets were grown in solutions containing 2 and 13 milliequivalents of nitrate ion in two control beds, in two beds with 100 milliequivalents of chloride, and in two beds with 200 milliequivalents of sulfate. Onions and alfalfa made in the order of 25 percent more growth in the low-nitrate than in the high-nitrate control; barley and beets showed an even greater advantage in the high-nitrate over the low-nitrate control. The yields of onions and alfalfa were nearly the same in the chloride and sulfate beds, and the barley yield was appreciably lower in the sulfate than in the chloride beds, but there was no clear evidence of a nitrate effect on the salt tolerance of any of these crops. The table beets, like the sugar beets of experiment 1, produced almost as well in 100 milliequivalents of chloride as in the control beds, and the nitrate advantage was retained. The injury of the table beets in the high-nitrate sulfate bed was substantial, corresponding to sulfate injury to sugar beets, and the nitrate advantage was marked; the yields of beets in the low- and high-nitrate control beds were respectively 100 and 176; in the chloride beds, 114 and 150; and in the sulfate beds, 71 and 141, all of the values being relative to the low-nitrate control. In each of the four crops the added nitrate depressed chloride accumulation in the sap and the added chloride depressed nitrate accumulation. The addition of sulfate had little effect on either nitrate or chloride accumulation.

A somewhat general question has been raised in connection with the interpretation of some of the older sand- and water-culture studies. Many of these studies were conducted before the necessity for adding elements such as manganese, boron, and zinc to nutrient solutions was recognized, and there is therefore the possibility that essential trace elements may sometimes have been introduced as impurities with the chloride or sulfate salts and thus have improved the growth of the plants, offsetting the toxicity of the salts in the lower concentrations.

There is little information upon which to base conclusions as to the relationship between transpiration rates and salt accumulation in the plant and the consequent injury. Muenscher (*23*), in general agreement with numerous earlier investigators, who in nearly all instances confined their laboratory measurements to the determination of total ash, found that the ash of barley, expressed in percentage of total dry weight of whole plants, varied but slightly whether the plants were grown under conditions of high or low transpiration and regardless of how transpiration was reduced. Hoagland and Broyer,[6] on the other hand, found higher concentrations of sodium and chloride ions in the expressed sap of barley plants grown in a dry chamber than in that of plants grown in a humid chamber. They also reported that bromide ion was taken up from culture solutions and moved into the roots, stems, and leaves of squash and cotton more rapidly under the influence of light and humidity conditions conducive to high transpiration rates than under those conducive to low transpiration rates.

Ahi and Powers (1) have observed the toxicity of sea-water mixtures to saltgrass and of sodium chloride to alfalfa when these plants were grown in water cultures in cold and warm greenhouses. The effect of temperature on salt injury as shown by their data was not marked when growth relative to the controls in the respective greenhouses was computed in terms of percentage growth reductions. The investigations of Hoagland and Broyer (15) and of Prevot and Steward (*27*), dealing with other factors affecting accumulation, likewise have a bearing on the general subject of salt accumulation.

The results of experiments dealing with the long-standing question of the role of chloride as an essential or beneficial element and with the effects of chloride introduced into soils with fertilizers are to some extent in contrast with those that have dealt with the problem of salt accumulation and toxicity under conditions of irrigation agriculture. The investigational handicaps in these inquiries are similar, and as a consequence the findings have been diverse and often conflicting. The fact that plant species and varieties are commonly so clearly distinct from one another in their nutritional requirements and preferences, in their tolerances, and in their environmental responses has contributed in a major way to the difficulties of formulating generalizations. The yields of flax, buckwheat, and potatoes have been shown to be reduced and the quality of tobacco to be inferior, under some conditions, when potassium chloride rather than potassium sulfate has been used as a

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[6] Unpublished data presented by D. R. Hoagland and T. C. Broyer at the twenty-second annual meeting of the Pacific Division of the American Association for the Advancement of Science, San Diego, Calif., June 21, 1938.

fertilizer. On the other hand, a number of crop plants have been found to respond favorably to moderate amounts of chloride. Extensive reviews of this literature are provided by Tottingham (*32*) and Lomanitz (18) and more recently by Shestakov and Shvindenkov (*29*, *30*) and by Masnewa (*21*). The findings of Garner et al. (11) on the reactions of tobacco to chloride are likewise pertinent.

Under the conditions that existed during the course of the outdoor sand-culture experiment, it was found that 100 milliequivalents of sulfate added as mixed sodium, calcium, and magnesium salts was about as toxic to dwarf milo, alfalfa, and cotton as 50 milliequivalents of chloride. Relations of this character have on several occasions suggested the possibility that the toxicity of chloride and sulfate might be related on the basis of equimolar concentrations or on the basis of equal electrical conductances or equal osmotic concentrations. It must be observed in this connection, however, that lemons withstood three or four times as many milliequivalents of sulfate as chloride, whereas beets withstood chloride better than sulfate. In other experiments it has been observed also that there are significant differences among plants in their reactions to both chloride and sulfate when these ions are added respectively as calcium, magnesium, and sodium salts; tomatoes, for example, even though accumulating little sodium (table 6), have been found to be substantially more tolerant to calcium chloride than to sodium chloride. In view of these diverse reactions and the specificity shown in ionic uptake by different plants, it seems improbable that chloride and sulfate toxicity can be evaluated on a simple physical or chemical basis.

SUMMARY

A series of crop plants was grown to maturity in each of six large outdoor sand cultures supplied with a base nutrient and with chloride and sulfate salts (50 percent as sodium) added, in milliequivalents per liter, as follows: Control, 50-chloride, 150-chloride, 50-sulfate, 150-sulfate, and 250-sulfate. The values for the growth of the plants in the 50-chloride bed and of the average of the plants in the 50- and 150-sulfate beds, measured as percentage of the controls, were respectively as follows: Lemon cuttings, 28 and 59; navy beans (seed), 39 and 45; dwarf milo (grain), 54 and 60; Chilean alfalfa (3 cuttings), 73 and 75; Acala cotton (seed cotton), 75 and 77; Stone tomatoes, 78 and 64; sugar beets (fresh roots), 98 and 80. Sulfate appeared to be about half as toxic as chloride to some plants, but the lemon was apparently four or more times as tolerant to sulfate as to chloride. Tomatoes and beets were more tolerant to 50 milliequivalents of chloride than to 100 milliequivalents of sulfate.

Barley, milo, and navy bean leaves were burned by chloride and sulfate salts, and occasional lemon leaves were burned. Alfalfa, cotton, tomato, and beet plants showed no burning of the leaves nor were there symptoms of diagnostic significance other than a reduction of leaf size in cotton and severe blossom-end rot of tomatoes.

The growth-depression curves showed no evidence of an abrupt point at which toxicity effects became pronounced. It was indicated instead that above some minimum concentration each successive unit of salt, if considered by itself, tended to produce a lesser depression in growth than the preceding unit.

The succulence of the crops, barley excepted, as measured by the quantity of sap expressed under standard conditions after freezing, was not influenced by the concentration of salt in the culture solutions.

Analyses of the expressed tissue fluids of the six crops examined showed much diversity in the proportions and quantities of ions accumulated in the sap. The ratios of concentration of salt constituents in the nutrient solution to the concentration in the sap of the control plants were high for nearly all ions. The base nutrient solution contained 0.6 milliequivalents of chloride, and the six crops growing in the control bed contained from 18 to 63 milliequivalents of chloride in their expressed sap. The addition of 50 to **150** milliequivalents of chloride to the base nutrient tended to produce a corresponding increase in the concentration of chloride in the expressed sap. Tenfold increases in the concentration of bases in the nutrient solutions by the addition of chloride salts and fourteenfold increases by the addition of sulfate salts in no case doubled the concentration of total bases in the expressed sap of any of these plants. Potassium accumulation was little affected by other ions. Cotton and tomatoes in all treatments had several times as much sulfur in their sap as the other plants. The hydrogen-ion concentration of the sap of a number of the plants was increased by chloride but not by sulfate.

On the basis of comparisons between electrical-conductivity measurements on the culture solutions and on the plant saps and the corresponding inorganic analyses, it is concluded that conductivity has little significance as a measure of the electrolyte content of expressed tissue fluids.

Increases in the osmotic pressure of expressed tissue fluids, resulting from the salt additions, tended to parallel the increases in the osmotic pressure of the culture solutions. The data do not support the presumptive reasoning that has sometimes led to the view that plants on saline substrates are injured because of the high osmotic concentrations of the substrate and consequent limitations in the rate of water intake.

Less water was lost by transpiration and evaporation, per unit of dry matter produced, from the 50-chloride and 50-sulfate cultures than from the control bed. The water requirements of the 150-chloride and 250-sulfate plant's exceeded those of the controls. The results point to the conclusion that the water requirements of plants growing on saline soils tend to be lower than those of plants on nonsaline soils but that this effect may be more than offset when the reduced growth causes an excessive exposure of plants to light and wind.

There was no blossom-end rot of tomatoes in the control bed, whereas 34 percent of the fruits in the 150-chloride bed and 78 percent in the 150-sulfate bed were affected. Unfavorable water relations due to high osmotic concentration in the solutions arc discounted as a probable cause, and some relation to calcium and magnesium accumulation is indicated.

Four greenhouse experiments were conducted on corn and tomatoes grown in water cultures with mixed calcium, magnesium, and sodium chlorides and with mixed sulfate salts. Chloride and sulfate concentrations above a few milliequivalents were injurious to corn. Tomatoes showed a maximum growth with 10 milliequivalents of chloride and with 5 milliequivnlents of sulfate. The growth-depression curves of both plants in both chloride and sulfate salts tended to flatten out as the concentrations were increased, showing a higher degree of toxicity per unit of salt in the low concentrations than in the high concentrations. Similar results were obtained in an experiment with wheat in water cultures to which sodium chloride was added. Increasing the concentrations of chloride and sulfate salts throughout the higher concentration ranges reduced the water requirements and increased the weights of roots relative to the weights of the entire plants.

Confirmation of the evidence of a beneficial effect of low concentrations of chloride ion on the growth of tomatoes as observed in the water-culture experiments was obtained in sand cultures. Tomatoes and cotton made respectively 35 and 81 percent more growth on the basis of green weight with 3 milliequivalents of chloride (106.5 p. p. m.) in the nutrient solution than with a trace of chloride.

The terms “critical concentration,” “limit of tolerance,” and “threshold values,” not infrequently appear in the salt-tolerance literature. These terms, which are borrowed from other biological fields, do not appear to be well suited to descriptions of the responses of plants to chloride and sulfate salts. There were no plant reactions or points on the injury curves in any of the experiments to which any of these terms were applicable. The limit of tolerance for any plant appears to be an intangible concept, since death takes place slowly over a range of concentrations, and on especially warm days plants growing in saline solutions may die rapidly.

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