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ALKALI TOLERANCE OF PLANTS CONSIDERED AS A PHENOMENON OF ADAPTATION

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FOREWORD

When an investigator of plant behavior observes an oft-repeated but somewhat obscure natural phenomenon, his first thoughts are, why is this and what is its underlying cause? In the absence of definite data, the tendency too often has been to formulate explanatory theories which do not explain, but rather tend to befog the issue. Almost invariably too hard work is made in attempting to explain a comparatively simple life process, the ultimate desire being usually to formulate definite mathematical expressions for bio-phenomena which of necessity under natural conditions vary as conditions vary, and hence we have such meaningless terms as "physiologically balanced nutrient solutions," "antagonism," and "the damming-out effect" of one ion for another.

The more simple the explanations and the less involved the contributing theories invoked, the more plausible do they become. The author of this bulletin gives us a straightforward, logical reason why plants tolerate more of one alkali salt than of another, and why plants vary among themselves in resistance to alkali poisoning; also why the calcium ion almost invariably has an ameliorating effect when concomitantly present, and why other ions do not. With plants, as with animals, we realize that there are certain fundamental traits that are fixed, while other more or less superficial characteristics may be changed almost at the will of the plant breeder, and within a few generations. Examples of the former are: The necessity for the 10 or 12 essential elements present in true solution and in ionic forms; the tendency of most plants to grow in a vertical position and with the leaves flat toward the sun; the tendency to grow toward the light, etc. Examples of changeable properties are, high or low fat, protein, or carbohydrate contents of fruits, and certain other flowering and fruiting propensities. The fixed characteristics are those which have been slowly formed during the untold ages through which the plant has passed in becoming adapted to present external, environmental conditions. The superficial characteristics have been more a matter of chance and are of less importance to the plant from the very essential viewpoint of propagation.

The paper which follows is unique in that it offers an explanation of alkali tolerance not heretofore generally considered.

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By J. F. Breazeale

INTRODUCTION

In popular conception, the term "alkali" carries with it the idea of the salts of sodium, together with and in small amounts, the salts of calcium and magnesium. It is true that of all the alkalies occurring in the soil, sodium salts are the most common, but there are many salts that may be considered as alkalies, other than the salts of sodium, calcium, and magnesium. Copper sulphate, for example, existing in small amounts, is just as much an alkali as is sodium chloride, and although not in evidence as an alkali crust, it is capable of doing much harm. In this bulletin the term "alkali" is used to designate any water-soluble salt in the soil.

When certain salts, sodium chloride or magnesium sulphate, for example, are added to soil or water cultures of most plants in increasing amounts, a concentration will be reached in which the plants will not grow. This concentration has been termed the "limit of endurance" or "alkali tolerance" of the plant, and this varies widely with plants of different species, and also, to a much less degree, with individuals of the same species. In western soils, where all the alkalies occur, and in different percentages, it is a matter of great importance to know what crop is best suited for growing in each alkali soil, or in each percentage of alkali. An accurate determination of the alkali tolerance of certain plants for the common salts is, therefore, of far-reaching importance economically, and so the energies of many investigators have been bent in this direction. This phase of alkali tolerance, that is, its relation to crop production, will not be discussed here. This bulletin is concerned with some of the essential reasons why plants react as they do when brought in contact with a more or less toxic salt.

To one who has worked on the subject of alkali in its relation to plant growth, and who has studied the literature on the subject, the lack of correlation in the work of investigators along this line is striking. It is almost impossible to repeat the work of another person and get comparable results. This lack of correlation is usually attributed to one of two causes—unskilled workmanship and too many variants. While these two factors unquestionably have played an important part in past investigations, there are other factors that heretofore have been overlooked. The same criterion has not even been used, and few of the investigators have thought alike upon any one phase of the subject. However, with skilled workers and the minimum of variants, the investigations have been handicapped by the absence of fundamental viewpoints.

ALKALI TOLERANCE OF A PLANT BUT A MEASURE OF THE LIMIT OF ENDURANCE OF ITS ENZYMES

Many investigators of plant tolerance have used root elongation as a criterion, and there is a possibility in the use of such a criterion that most workers have failed to consider, and that is, in measuring the toxic limit of a plant for alkali, we are probably but measuring the limit of endurance of some of its growth enzymes. The amount of magnesium sulphate, for example, that will stop the root development of a plant, seems to be the amount of that salt that is required to kill the enzymes upon the root-tip, that are concerned with growth. Therefore, in dealing with alkali tolerance, when root elongation is used as a criterion, we are probably not dealing with the destruction of vegetative cells as much as we are with enzymes that affect their growth. This idea has been brought out by much investigation.

Kearney and Harter* in their work upon alkali tolerance, found that the age of the seeds of lupine had an important effect upon the limit of endurance of seedlings, when grown in pure salt solution. This difference was not noticeable when calcium was present in the culture solutions. it has the greatest amount of certain enzymic activity. This indicates will endure less alkali than will fresh seeds, and that light and temperature also affect the limit of endurance of plants. Plants will endure more alkali in the dark than they will in the light. The limit of endurance is also affected by the age of seedlings, the root-tip of a wheat plant seems to be most sensitive when 5 to 9 days old, this period being the time it has the greatest amount of certain enzymic activity. This indicates that, in alkali tolerance we are probably not dealing with the root-tip as vegetative tissue, as much as we are with the enzymes that affect its growth.

EXPERIMENTS WITH SEEDLINGS

In the work that will be reported, the elongation of the primary radicals was used as a criterion. The seedlings of the cereals were grown upon perforated aluminum discs that were floating in pans of tap water. Corn, citrus, and other seedlings were either sprouted between wet cloths or grown in sand beds, and when the primary radicals had

*The Comparative Tolerance of Various Plants for the Salts Common in Alkali Soils U. S D A Bureau of Plant Industry, Bull 113, 1907.

reached a length of about 2 cm. the seedlings were removed from the seedbed, their roots dipped into a thick magma of carbon black, and then placed under observation in the alkali solutions. The carbon formed little "black boots" about one-half cm. long over the end of each root. Any elongation of the roots then could be detected easily by a break in the black band just back of the rootcap.

TOXIC LIMITS OF CALCIUM HYDROXIDE AND SODIUM HYDROXIDE

As a result of many determinations, the limit of endurance of corn seedlings for calcium, when added as calcium hydroxide, was found to lie between 150 and 175 parts per million in solution, while the same corn seedlings will endure a concentration of twice that amount, or about 300 parts per million of sodium, as sodium hydroxide. This same phenomenon is true with cotton, wheat, and citrus seedlings and probably many other plants, that is, calcium hydroxide is much more toxic to them than is sodium hydroxide. The toxic limit of citrus seedlings, for example, is about 80 parts per million of calcium, as calcium hydroxide, and about 175 parts per million of sodium, as sodium hydroxide. Caustic soda is known to be much more destructive to organic matter than is calcium hydroxide. There is another reason underlying this phenomenon other than the effects of these bases upon growth enzymes, that will be discussed later.

RESISTANCE OF GROWTH ENZYMES TO SOLUTIONS OF SODIUM HYDROXIDE

The limit of endurance of wheat seedlings for sodium hydroxide, is about 250 parts per million. A solution slightly above this concentration, or sufficiently strong to stop all root elongation, was prepared, and six sets of wheat seedlings were placed in this solution. Set No. 1 was allowed to remain in the alkaline solution for 1 hour, set No. 2 was allowed to remain for 2 hours, set No. 3 for 3 hours, set No. 4 for 4 hours, set No. 5 for 5 hours, and set No. 6 for 24 hours. At the end of each period as indicated, the seedlings were taken from the alkaline solution, placed in tap water and allowed to remain overnight. In Table I are shown the results of the experiment.

It thus appears that wheat seedlings are able to remain in a toxic solution of sodium hydroxide for at least 2 hours, without any apparent injury. It required about five hours, under the conditions of the experiment, for the alkali to penetrate the root-tip and to destroy the enzymes that are associated with root elongation.

When toxic salts are added to seedling cultures in concentrations of the limit of endurance of the plant, the root-tips cease growing, but do not slough off. The vegetative cells do not seem to be ruptured. Usually another root system is developed that is able to withstand the concentration of alkali. The growth enzymes of some roots are more resistant than are those of other roots, even on the same plant.

This experiment indicates that it is probably the destruction of enzymes and not necessarily the destruction of vegetative tissue, that is most concerned in the alkali tolerance of plants.

TABLE I.—RESISTANCE OF ENZYMES TO SODIUM HYDROXIDE

Number	Time in NaOH solution	Condition of roots after 18 hours in tap water
Control	0 hrs.	Good growth
1	1 hrs	Good growth
2	2 hrs	Good growth
3	3 hrs.	Slightly decreased growth
4	4 hrs.	Much decreased growth
5	5 hrs.	No growth
6	24 hrs.	No growth

ORDER OF TOXICITY OF ALKALI SALTS

From all the work that has been done on the limit of endurance of plants for alkali, regardless of what criterion has been used, there seems to be a fairly definite order of toxicitiy for all salts. The salts of the heavy metals, copper sulphate or mercuric chloride for example, are very toxic, and rank high in the table, while the salts of calcium, calcium sulphate or calcium nitrate, are not in ordinary concentrations toxic, and rank low in the table. The sodium salts are moderately toxic and so on. The salts that are common in alkaline soils, tend to arrange themselves in approximately the following order:

1. Magnesium sulphate
2. Magnesium chloride
3. Sodium carbonate
4. Sodium bicarbonate
5. Sodium chloride
6. Sodium sulphate
7. Calcium sulphate

The position of each salt in such a table of toxicity will probably vary with the plant used, and probably to a certain extent the order will vary with each investigator, but had we the methods of eliminating variants and of making our determinations accurately, no doubt a table of toxicity could be arranged that would be almost as definite as is Mendeleeff's table of atomic weights. This order of toxicity seems to have been gradually developed by the species through a long period of time, so that each salt now occupies its proper and definite place. In developing this order, the plant appears to have been directed by the same principles that have directed every other phase of its development. *Therefore, it looks as if the toxicity of any salt is determined by the units of time that the plant has come in contact with that salt during its long period of adaptation.*

Plants have come in contact with gypsum a great many times during this period, therefore, ordinary plants will tolerate a saturated solution of that salt. Plants have met with mercuric chloride and copper sulphate only upon rare occasions, and, therefore, these salts are extremely toxic. Most plants have come in contact with sodium chloride rather frequently, therefore, in the presence of calcium, they can endure a concentration of about one percent of that salt, and so the list might be added to indefinitely. It is probably possible to predict the frequency of the occurrence of a certain salt in the soil solution during the age of adaptation of a plant, if we know the limit of endurance of the plant for that particular salt; or knowing the frequency of the occurrence of a certain salt in the soil solution, we should be able to predict the degree of toxicity of that salt.

Calcium and magnesium are very much alike chemically, and it is reasonable to suppose that they should react similarly toward plants, but they do not. Magnesium sulphate is much more toxic than is calcium sulphate, and for the probable reason that the plant has met calcium sulphate 10 times during its period of adaptation, where it has met magnesium sulphate only once. Nearly all of the lower oxides, or "ous" salts, ferrous sulphate for example, are more toxic than are the higher oxides or "ic" salts—ferric sulphate. This is true probably because the "ous" salts exist in nature only in exceptional cases, as the oxygen of the air tends to oxidize every salt to its limit.

TOXIC ACTION OF CALCIUM HYDROXIDE AND SODIUM HYDROXIDE

Referring to the experiments with the relative toxicities of calcium hydroxide and sodium hydroxide, not one scientist in a hundred would guess that caustic lime is twice as toxic as is caustic soda, but if the hypothesis that the toxicity of a base, acid or salt, is dependent upon the number of times that the plant has come in contact with it, the results are exactly what one might expect. The ordinary calcium salts, calcium sulphate or calcium carbonate, are very abundant in nature, but caustic lime (calcium hydroxide) does not exist in appreciable amounts under ordinary circumstances. Caustic soda (sodium hydroxide) does exist, for when we drop phenolphthalein into a solution of sodium carbonate (black alkali) and get a red color, we get the reaction for sodium hydroxide, that is, for the OH ion. When sodium carbonate goes into solution in water, it is hydrolyzed with the formation of a certain amount of sodium hydroxide, so the plant, in becoming adapted to black alkali, also became adapted to sodium hydroxide. We might, therefore, expect the plant to be less affected by and more tolerant of sodium hydroxide than of calcium hydroxide, which is true.

AMMONIA AND ADAPTATION

Recently determinations were made of the limit of endurance of plants for ammonia gas dissolved in water, and a concentration of 40 parts per million was found sufficient to kill seedlings of corn and cotton. This is cited in order to show the possibility of predicting from the behavior of a plant, what the natural conditions must have been during its period of adaptation. The salts of ammonia, ammonium chloride or ammonium sulphate for example, are not very toxic, indicating that the plant has probably met with them frequently, but ammonia as a hydroxide is very toxic and ranks with the salts of some of the heavy metals. During the processes of nitrification and denitrification, and the formation of reduction products from nitrates and nitrites, some salts of ammonia could readily be evolved, but any intermediate products in the shape of a gas or of an hydroxide must have existed in extremely small amounts.

STIMULATION AND ADAPTATION

It is a well known fact that nearly all alkalies, even of the most toxic compounds, are stimulating to plants, when administered in small or proper amounts. This phenomenon is so general that hardly an exception can be recalled. If a certain salt, the base of which is some heavy metal, for example, is toxic in a concentration of 10 parts per million, it will quite likely be stimulating in a concentration of 1/10 part or less per million. The soil in which ordinary plants have become adapted to salts is such a heterogeneous mixture that hundreds of what are ordinarily considered as toxic compounds are likely to occur in it, although they may exist in extremely small amounts. The plant has become adapted to this condition, as is indicated when it is placed in a similar medium under artificial conditions. It requires what it has been accustomed to and it reacts favorably when given those things in culture media that occur in the normal soil solution. Most plants of economic importance have developed in humid areas, where we always find a certain amount of active organic matter in the soil solution. When such plants are transferred to arid regions where organic matter is usually lacking in the soil solution, ordinarily they do not thrive unless given a certain amount of organic matter. When given plenty of water, active organic matter seems often to be the limiting factor in arid and semi-arid agriculture, and apparently for the reasons just cited. The marked results that follow the application of manure or certain other forms of organic matter can scarcely be explained upon the basis of the plant food that they contain or upon their effect on the mechanical condition of the soil.

A plant appears to be able to become adapted to, and to establish a definite limit of endurance for a salt, without ever having come in contact with that salt in toxic concentrations. It must establish a toxic limit far in advance of the concentration of the alkali that is commonly met with, else the species would not have existed until now. There is probably a definite ratio between the concentration of a salt that is met with in daily growth, and its toxic limit. Furthermore, it seems possible for a plant to become adapted to a salt with which it has never come in contact, even in small amounts. Experience teaches that a plant may become adapted to one salt that is representative of a large class of salts.

MUTATIONS AND THE ORDER OF TOXICITY

It might also be suggested that a mutation may upset the order of toxicity, but this is seriously doubted. A mutation may cause a change with respect to the absolute amount of a salt that is required to prohibit growth, but there is only a slight possibility that the relative order of the salts will be changed. Calcium sulphate will probably remain at the bottom of the list, and magnesium sulphate in a position nearer the top. We should not expect calcium sulphate and magnesium sulphate to exchange places. Their relative positions seem fundamental and fixed.

There may be many apparent exceptions to this hypothesis, when it is considered in detail, but it is doubtful whether our present knowledge of the subject will justify us in calling those exceptions. It is possible that the individual plants under stress react differently from what they would do under ordinary conditions. This is true even in the behavior of chemical elements. Salts that lie close together in the table of toxicity, sodium chloride and sodium sulphate for example, may overlap one another, or under certain conditions, may even change places, but this must be included in our limit of error, which of necessity must be wide. Individual variation may play an important part, but these cases will probably be the exceptions and not the general rule. It certainly seems possible to arrange the great body of alkali salts in a table, in positions depending upon the units of time that the plant has come in contact with them during its period of adaptation.

IS THE TOXICITY DUE TO THE MOLECULE OR TO THE ION IN SOLUTION?

It is a matter of fairly common belief that the toxicity of an acid or a salt depends largely upon the amount of the positive ions present

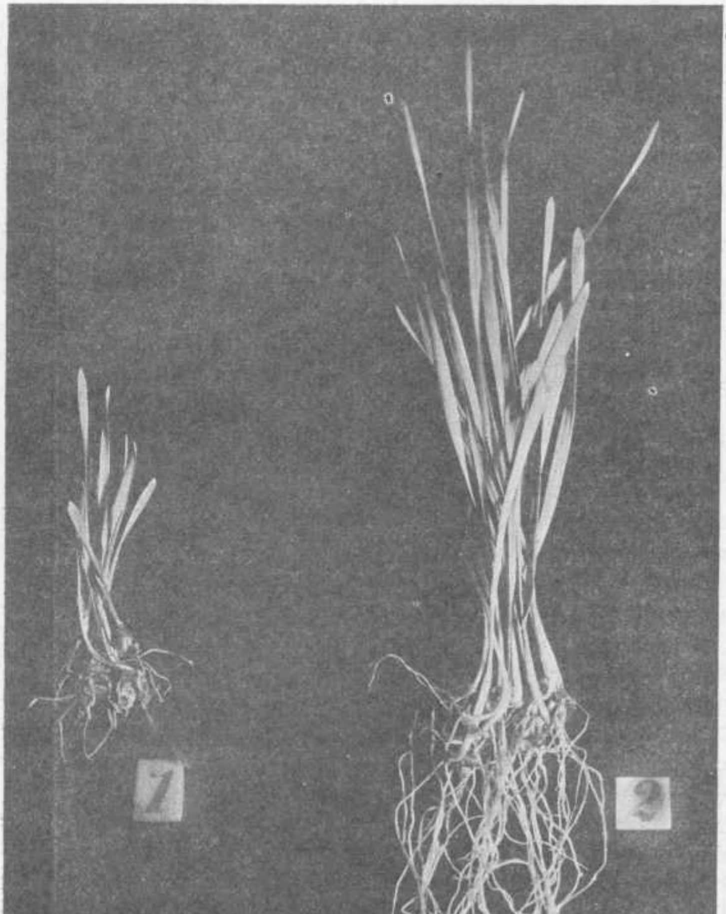

Fig. 1.—Wheat seedlings grown in pots of sand and watered exclusively with: (1) 4,000 parts per million sodium chloride; (2) 4,000 parts per million sodium chloride with 50 parts per million calcium oxide.

in solution, that the toxicity of hydrochloric acid, for example, is largely a function of the H ion, while that of sodium sulphate may be attributed to the Na ion. This seems to be true in some cases, but there are so many exceptions to it that the hypothesis seems hardly tenable. Calcium hydroxide is very toxic, while plants can grow vigorously in a saturated solution of calcium sulphate. Sodium carbonate is toxic while sodium nitrate is not. Calcium hydroxide is more toxic than is sodium hydroxide, while calcium sulphate is much less toxic than sodium sulphate and the list could be added to almost indefinitely.

The degree of toxicity of a salt is not an accidental phenomenon, neither is it determined by physical or chemical laws. It is probably a biological phenomenon, and it has been established by the plant during its era of adaptation. Therefore, while in some cases, toxicity may depend upon the ion, in a great many other cases it seems to be due to the molecule rather than to the ion.

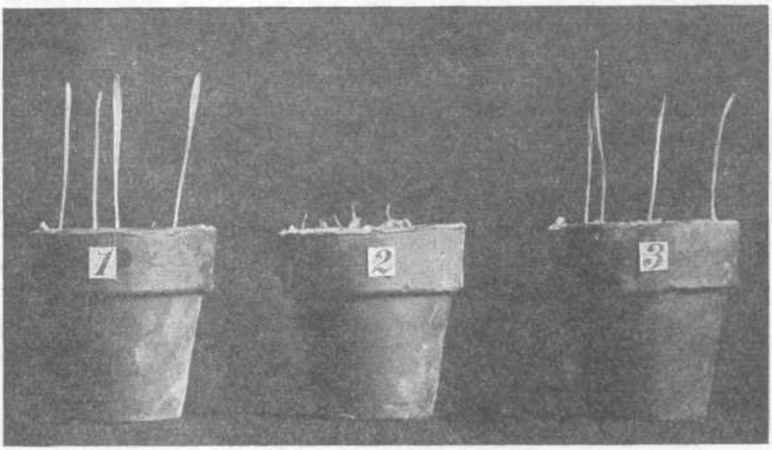

Fig. 2.—Wheat seedling grown in pots of pure aluminum hydroxide and watered exclusively with: (1) Distilled water; (2) 4,000 parts per million sodium chloride; (3) 4,000 parts per million sodium chloride with 50 parts per million calcium oxide.

THE AMELIORATING EFFECTS OF SMALL AMOUNTS OF CALCIUM

When cultures of wheat seedlings are grown in pure, distilled water, and pure sodium chloride is added to these cultures in increasing amounts, the plants will grow and their roots will elongate until a concentration of about 4,000 parts per million is reached, when the roots will cease to elongate. This is the "limit of endurance" for wheat in sodium chloride solutions. If, however, a small amount of a soluble calcium salt is added to the sodium chloride solutions the concentration of the sodium chloride may be increased to over 10,000 parts per million before the limit of endurance is reached. This phenomenon is more strikingly shown with some other plants than with wheat, although their limit of endurance of alkali may not be the same. This ameliorating effect of calcium in culture solutions is so well known that it needs no data and no comment. However, the fact that the phenomenon is true in certain other culture media is not so well known.

All soils contain enough calcium to mask this reaction, but with cultures growing in any medium that contains no calcium, such as quartz flour, pure sand, aluminum hydroxide, or carbon black, the same phenomenon is noticed. In figure 1 is shown the beneficial effects of calcium upon wheat seedlings that were grown in pure sand and watered with a solution of sodium chloride. In figure 2 is shown the effect of calcium upon cultures that were grown in aluminum hydroxide and watered with sodium chloride solution, and in figures 3 and 4 is shown the effect of calcium upon cultures that were grown in carbon black and watered with sodium chloride solution.

This ability of calcium to ameliorate or neutralize the toxic effect of alkali salts is one of the most interesting phenomena in plant physiology, and many explanations have been proposed. If alkali tolerance of plants is largely a phenomenon of adaptation, and if the degree of toxicity of any particular salt is determined by the units of time that the plant has come in contact with that salt during its age of adaptation, it appears that the ameliorating effect of calcium above referred to, may also be classified as a phenomenon of adaptation, and that immunity to alkali in the plant kingdom, and immunity to disease in the animal kingdom, are closely allied phenomena.

CALCIUM CARBONATE AND ALKALI TOLERANCE

In the arid and semi-arid regions of the West, where alkali is likely to occur, calcium carbonate is very prevalent. Hilgard says: "All arid soils are calcareous" and, barring extreme cases, he is probably correct. The solubility of calcium carbonate in pure water is only about 7 or 8 parts per million, this solubility, however, is increased by the presence of carbon dioxide. Bearing in mind the wide distribution of calcium carbonate and its low solubility, the plant, in becoming adapted to alkali, was almost sure to do this in the presence of calcium, even though it occurred in very small amounts. The amount of calcium in solution might have varied from a few parts per million in the case of calcium carbonate, to several thousand parts per million when gypsum or some other more soluble calcium salt occurred in the soil, but certainly some calcium was always present.

Fig. 3.—Wheat seedlings grown in pots of carbon black and watered exclusively with: (1) Distilled water; (2) 1,000 parts per million sodium chloride; (3) 2,000 parts per million sodium chloride; (4) 3,000 parts per million sodium chloride; and (5) 4,000 parts per million sodium chloride.

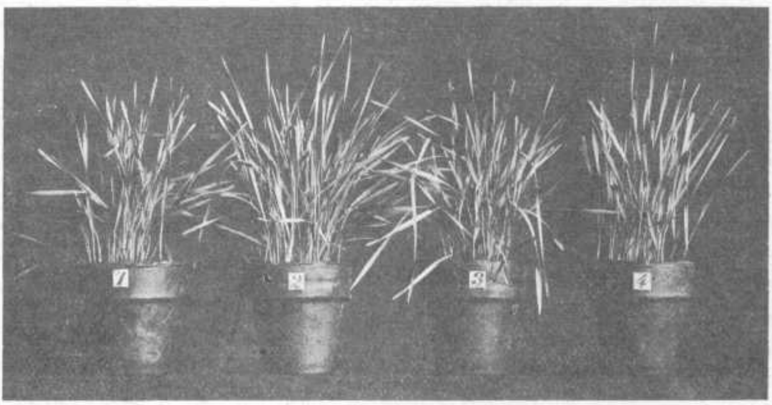

Fig. 4.—Wheat seedlings grown in pots of carbon black and watered exclusively with: (1) Distilled water; (2) 1,000 parts per million sodium chloride with 50 parts per million calcium oxide; (3) 2,000 parts per million sodium chloride with 50 parts per million calcium oxide; (4) 4,000 parts per million of sodium chloride with 50 parts per million calcium oxide.

Sodium chloride is probably the most common alkali salt that is met with in agricultural work. It has been shown* that when sodium chloride comes in contact with calcium carbonate, a reaction occurs with the formation of sodium carbonate, black alkali, and calcium chloride. This brings a calcium salt, calcium chloride, into solution, and we are now not dealing with the solubility of calcium carbonate, but with the more soluble calcium chloride. The plant in becoming adapted to sodium

*Breazeale, J. F. "Formation of Black Alkali in Calcareous Soils," Jour. Agr. Res. Vol. X, No. 11. 1917.

chloride will do this in the presence of more or less calcium chloride. The maximum amount of calcium carbonate that can be dissolved by sodium chloride in the presence of carbon dioxide, under ordinary soil conditions, is only about 1,300 parts per million. When sodium sulphate occurs in the soil as an alkali it will bring not 1,300, but nearly 7,000 parts per million of calcium carbonate into solution. It will be seen then that the alkali, sodium sulphate, dissolves and makes available to plants, about five times as much calcium as does sodium chloride, and a plant in becoming adapted to sodium sulphate will be likely to come in contact with five times as much calcium as it will when becoming adapted to sodium chloride. We might, therefore, expect a plant affected with sodium sulphate poisoning to react more readily to an application of gypsum than one affected with sodium chloride poisoning. This was predicted from theoretical curves, and Kearney and Harter's work* indicates it.

The ameliorating effect of calcium, while very pronounced with both sodium chloride and sodium sulphate, is not nearly so marked in the case of sodium carbonate or black alkali, and the reason seems evident. In its age of adaptation, when the plant has encountered black alkali, there was necessarily very little calcium present in the solution. If gypsum or any soluble lime salt is added to a solution of sodium carbonate, or to a black alkali soil, a reaction will take place with the formation of calcium carbonate and sodium sulphate, and thus a greater part of the calcium will be removed from the solution. The black alkali soil can, therefore, contain but a very small amount of calcium in solution, and so the plant, when affected with black alkali poisoning, does not "anticipate" the presence of any appreciable amount of calcium, and consequently does not react to any great extent when given an application of calcium. However, as black alkali practically always occurs in the presence of calcium carbonate, there is always a very small amount of calcium in solution, so, theoretically, the plant should "anticipate" a little calcium and would react only a little when calcium appears in the cultures, and this is exactly what happens.

Magnesium, as magnesium sulphate or magnesium chloride, is another form of alkali that sometimes occurs in mixtures. Both of these salts act in very much the same way toward plants, so only one, magnesium sulphate, will be considered. Kearney and Harter found that the limit of endurance of lupine for magnesium sulphate is raised from 420 parts per million to 24,000 parts per million, or nearly 60 times, while the limit of endurance of alfalfa is raised over 300 times, by the presence of

*Loc. cit.

gypsum. The interpretation of these phenomena seems to be that, in nature, the magnesium in the common minerals usually occurs associated with calcium, the calcium nearly always predominating, so, in becoming adapted to magnesium it is more than probable that the plant did so in the presence of a large excess of calcium, and, if poisoned by magnesium under artificial conditions, it would be likely to require conditions approaching those of its native habitat for successful growth.

ORDER OF TOXICITY OF ALKALI SALTS AS AFFECTED BY CALCIUM

In dealing with the ameliorating effect of calcium upon the common alkali salts it seems possible that the salts may be arranged in a definite order, the highest place in the list being occupied by the magnesium salts for the reason that they have been constantly associated with a large excess of calcium, and the lowest place in the list being occupied by sodium carbonate because it has been associated with very little soluble calcium. If enough data on the ameliorating effect of calcium upon the limit of endurance of plants for all alkali salts were available, the data could probably be arranged in the form of a table from which one might get a definite idea of the probable occurrence of calcium with these salts in the locality where the plant under consideration had become adapted.

Thus, it seems that the plant in past ages, in becoming adapted to alkali, always had a certain amount of calcium present, and now, when placed under stress, it requires a condition approaching that to which it is accustomed. This seems a natural and most reasonable way of looking at this phenomenon. The much discussed "physiologically balanced solution," is the solution that the plant has become adapted to during its ages of development.

IMMUNITY AND ADAPTATION

The Indians of the Great Southwest are very susceptible to tuberculosis, and this has been attributed to the fact that tuberculosis is a new disease among them, and that they have not yet developed an immunity to it. This seems to be true with other diseases than tuberculosis and with other races than Indians. The Hawaiians are fast being decimated by new diseases. On the other hand, the white race seems to be wearing out many such diseases, as measles and smallpox, by developing an immunity to them. This immunity may be conceived of as a definite chemical compound in the blood of the individual. Certain it is that immunity to disease is very pronounced in the animal kingdom, and it seems probable that it is but a phenomenon of adaptation.

To the plant, a salt such as sodium chloride, when accompanied by a little calcium, is an old disease and may be overcome, but sodium chloride without calcium is a new disease for which no immunity has been developed. It is the opinion of the writer that alkali tolerance in plants depends largely upon immunity, which immunity is determined by the units of time that the plant has come in contact with the salt or mixtures of salts during its period of adaptation.

EXPERIMENTAL WORK WITH WHEAT SEEDLINGS

The writer has demonstrated repeatedly that, if wheat seedlings are first sprouted in distilled water and then placed in a 5,000-parts-per-million solution of sodium chloride, they will die. However, if the seedlings are first placed in a weak solution of calcium sulphate for a few days, then washed free from calcium and placed in the same 5,000-parts-per-million salt solution they will grow quite readily. There seems to be a "carry-over" effect from the time when calcium is present to a time when calcium is absent and when it is most needed. This suggested the following experiment:

Fifteen large enameled pans, each holding about 2,500 cc., were filled with solutions as described in Table II, and 500, or more, wheat seedlings were placed on perforated aluminum discs, each floating in one of these solutions. These solutions were then treated as described in Table II, and the cultures were kept under observation for 10 days. In order that the table may be more easily understood, the numbers were divided into five sets, A, B, C, D, and E.

TABLE II—BEHAVIOR OF THE WHEAT SEEDLINGS WITH THE VARIOUS TREATMENTS NOTED.

No.	Treatment	Condition of plants after 10 days
	A	
1.	Plants grown in distilled water	Good
2.	Plants grown in 1 percent pure sodium chloride	Dying
3.	Plants grown in 1 percent pure sodium chloride together with 30 p.p.m., Ca, as calcium sulphate	Good
	These results indicate that a concentration of 1 percent of pure sodium chloride alone, is sufficient to kill seedling of wheat, but that if 30 p.p.m. of calcium is present in addition to the sodium chloride, the latter salt will not be toxic.	
	B	
4.	Plants grown in distilled water for 1 day and then transferred to 1 percent sodium chloride	Dying
5.	Plants grown in 30 p.p.m. Ca, as $CaSO_4$, for 1 day then transferred to 1 percent sodium chloride	Very poor
6.	Plants grown in distilled water for 1 day, then transferred to 1 percent sodium chloride with 30 p.p.m. Ca	Good
	It seems as if wheat seedlings, when grown for even 1 day in a solution of 30 p.p.m. of calcium will become slightly immune to sodium chloride poisoning.	
	C	
7.	Plants grown in distilled water for 2 days then in 1 percent sodium chloride	Dying
8.	Plants grown in 30 p.p.m. Ca for 2 days, then transferred to 1 percent sodium chloride	Poor

9. Plants grown in distilled water for 2 days then in 1 percent sodium chloride with 30 p.p.m. Ca .... Good

Wheat seedlings when grown for 2 days in a solution of 30 p.p.m. calcium, before being placed in a toxic solution of sodium chloride become partially immune to sodium chloride.

D

10. Plants grown in distilled water 4 days, then in 1 percent sodium chloride .... Dying
11. Plants grown in 30 p.p.m. Ca for 4 days then in 1 percent sodium chloride .... Fairly good
12. Plants grown in distilled water for 4 days then in 1 percent sodium chloride with 30 p.p.m. Ca .... Good

Wheat seedling when grown for 4 days in a solution of 30 p.p.m. calcium become partially immune to sodium chloride.

E

13. Plants grown in distilled water for 6 days then in 1 percent sodium chloride .... Dying
14. Plants grown in 30 p.p.m. Ca for 6 days, then in 1 percent sodium chloride .... Good
15. Plants grown in distilled water for 6 days, then in 1 percent sodium chloride with 30 p.p.m. Ca .... Good

It appears that wheat seedlings, when grown for 6 days in a solution of 30 p.p.m. calcium as calcium sulphate before being placed in a 1-percent solution of sodium chloride, become practically immune to sodium chloride poisoning at that concentration.

When running the foregoing culture solutions, every effort was made to eliminate completely traces of calcium from the cultures where it was supposed to be absent. When removing the cultures from the dilute calcium sulphate solutions before placing them in the toxic solutions of sodium chloride, the plants were washed thoroughly and allowed to stand in distilled water for 1 hour before being transferred. In this way there was no mechanical transfer of the calcium sulphate into the sodium chloride solutions. A few parts per million of calcium are sufficient to mask all results and it is no easy matter to eliminate all traces of this element. The culture pans, aluminum discs, and the wheat seeds were washed with dilute acid and then washed with distilled water before being used. Dust moves with air currents and is likely to settle in the culture pans; since these experiments were conducted in a locality where calcareous soils occur, the cultures were kept covered and protected from this source of error.

Briefly summing up the results of this and of duplicate experiments, it follows:

1. That wheat seedlings are killed by a concentration of 1 percent of pure sodium chloride when no calcium is present. See numbers 2, 4, 7, 10, and 13.

2. That seedlings will endure 1 percent of sodium chloride, provided a small amount of calcium is always present. See numbers 3, 6, 9, 12, and 15.

3. That seedlings, if grown 1 or 2 days in a dilute solution of calcium, when transferred to a 1-percent solution of sodium chloride, while showing some immunity, will not withstand this concentration of salt. See numbers 5 and 6.

4. That seedlings, if first grown 4 or more days in a weak solution of calcium, will become practically immune to a 1-percent solution of sodium chloride. See numbers 11 and 14.

After 10 days observation, 100 seedlings were taken from each of the culture pans, washed, and analyzed for calcium. A few of these analyses are given in Table III.

TABLE III.—AMOUNT OF CALCIUM FOUND IN LOTS OF 100 WHEAT SEEDLINGS FROM THE VARIOUS CULTURE PANS.

No.	Treatment	Grams Ca in 100 plants
1.	Plants grown in distilled water	.0337
5.	Plants grown in 30 p.p.m. Ca, as $CaSO_4$, 1 day then in 1 percent sodium chloride	.0303
6.	Plants grown in distilled water 1 day, then in 1 percent sodium chloride with 30 p.p.m. Ca	.0340
14.	Plants grown in 30 p.p.m. Ca for 6 days, then in 1 percent sodium chloride	.0349

There seems hardly any evidence, from the results of these analyses, that the plants absorbed enough calcium from solutions 5, 6, and 14, to be detected. The original seeds, or the plants that were grown in distilled water, showed .0337 gram calcium. One of the other sets, No. 5, showed even a less amount, while the other two sets showed only slight increases over the control. Even the plants that were grown in cultures 14 and 15, (Table II), that gave such striking reactions to applications of calcium, showed little or no indications by their analyses that they had absorbed any calcium. It is reasonable to suppose that a plant grown for even a few days in a weak solution of gypsum, must necessarily absorb some calcium, but the amounts absorbed in the above experiment must have been exceedingly small, otherwise they would have been detected in the chemical analyses of the plants.

In work previously reported* it was shown that the presence of calcium did not hinder the absorption of sodium salts by the plant. Plants that were grown in solutions of sodium chloride and sodium sulphate, with small amounts of calcium present, absorbed as much, if not more, of the sodium salts than did plants that were grown in solutions of sodium salts that contained no calcium. The phenomenon is not due to the "damming-out" of the toxic salt. No satisfactory explanation has yet been

*"Effect of Lime Upon the Sodium Chloride Tolerance of Wheat Seedlings," J. A. LeClerc and J. F. Breazeale. Jour. Agr. Res. Vol. XVIII, No. 7. 1920.

offered for the effect of small amounts of calcium upon the toxic properties of other salts.

When wheat seeds are placed in distilled water, preparatory to germination, some salts will exude from the seeds before the plumules and radicals appear. Potassium and phosphorus predominate in these exudations, but small amounts of calcium probably in organic combination, also come out. The writer has never observed that this exuded calcium has any effect in overcoming alkali poisoning. It seems as if calcium must be in an inorganic form in order to be able to ameliorate the toxic action of alkali. Anti-toxines must themselves be poisons, or else they would not be anti-toxines. A compound cannot be a food and at the same time an anti-toxine. It seems as if the inorganic and not the digested organic calcium is required by the plant when suffering from alkali poison.

SUMMARY

For many years the writer has been studying problems pertaining to alkali, both in its relation to practical agriculture and from a purely scientific standpoint, and the evidence is not wanting that the whole problem of alkali tolerance centers on a phenomenon of adaptation. It is true that such an hypothesis does not necessarily explain all the phenomena, but it does seem to bring the matter one step nearer the truth.

The fact that a wheat plant is killed by a solution of 1 part per million of copper, and that it will grow vigorously in a saturated solution of gypsum, is not an accidental phenomenon. The fact that a plant requires calcium even in minute quantities, when growing in the presence of an alkali, is not surprising. These facts are expressions of the conditions that the plant was subjected to during its age of adaptation. In all probability, if the plant had met copper sulphates frequently and in increasing amounts, and had never met gypsum during this age, the effect of these two salts would now be reversed—copper sulphate would be practically harmless, while gypsum would be toxic. If the plant had met pure sodium chloride instead of a mixture of sodium chloride and some lime salt, the pure salt would not now be so toxic. The plant in its native habitat was in a state that approached equilibrium with all the forces of nature, and had it not been in such a state it could not have continued to exist to this time. Every plant is but a product of environment, its likes and dislikes or its individualities were worked out ages ago and in the most reasonable way. The fundamentals are established and all in response to simple natural laws. The plant breeder may, therefore, modify certain superficial characters, for example the fruiting propensities of a plant, but the fundamental likes and dislikes yield slowly to the methods of the breeder.

CONCLUSIONS

1. The limit of endurance of a plant for alkali salts seems to be determined by the amount of alkali that is required to kill the enzymes of the roots, that are concerned with growth.

2. There appears to be a definite order of toxicity of alkali salts, and the position of each salt in the order of toxicity depends upon the number of units of time that the plant has come in contact with the salt during its period of adaptation.

3. The presence of calcium, even in minute amounts, increases enormously the tolerance of wheat seedlings for sodium chloride and other alkalies.

4. Plants are able to utilize calcium at one period, and this calcium may be effective in overcoming alkali at a later period.

5. Plants may be inoculated, or "immmunized" against alkali, with calcium, just as readily as animals may be inoculated or vaccinated against certain diseases. Alkali tolerance in plants and immunity to disease in animals are closely allied phenomena, that is, they are both phenomena of adaptation.

6. A "physiologically balanced" solution may be defined as a solution that the plant became accustomed to during its era of adaptation.