RELATION OF NUTRIENT SOLUTION TO COMPOSITION AND REACTION OF CELL SAP OF BARLEY

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In recent years considerable attention has been given to the cell sap from different plants, especially as influenced by varying soil and climatic conditions. Some very interesting general relations have been brought out, but in these experiments it has not been possible to ascertain or control the exact concentration and composition of the soil solution. McCool and Millar (4), however, have made numerous measurements of the freezing point depressions of the cell sap of both tops and roots of plants growing in soils and nutrient solutions of varying osmotic pressure. These researches have shown clearly that the sap of the plant, particularly of the roots, reflects the concentration of the nutrient solution, whether in the soil or in water cultures.

Comparatively few measurements of the conductivity of the cell sap have been made, although some data concerning this point are quoted by Atkins (1). The H ion concentration and chemical analysis of the sap have received still less study, yet all these determinations are of the greatest importance in soil fertility investigations. The total osmotic pressure in the plant is known to be dependent to a considerable extent on intensity of photosynthetic action, as well as on the nutrient solution, while the inorganic constituents may well have a more direct relation to the surrounding media.

For a number of years this laboratory has been engaged in the investigation of the relation between the growth of the barley plant and the composition and concentration of the soil solution as shown by analyses of water extracts and freezing point determinations by the method of Bouyoucos and McCool (2). The work with soils has made it evident that the soil solution is of paramount importance in its effect on crop growth, while, on the other hand, the plant has a marked influence on the concentration and composition of the soil solution. It soon became apparent that the elucidation of these difficult relationships would require further study by the methods of water and sand culture, which may be subjected to more rigorous control. It is thought that some of the data pertaining to the cell sap of plants from these various soil, water, and sand culture experiments are worthy of a brief discussion at this time.

The soils were kept in large tanks under controlled conditions as described by STEWART (6). The technique of the water and sand cultures will be described elsewhere. The procedure was designed to place, so far as possible, no limitation on the growth of the plant other than the variables under investigation. The nutrient solutions were made to have a composition similar to that of the soil extracts with respect to the important elements. Various concentrations of both acid and neutral reaction were employed. In each concentration acid and neutral solutions had an almost identical osmotic pressure, and the relation between the various ions was very similar. The reactions were governed by the hydrolysis of the various potassium phosphates used.

The procedure employed in obtaining the cell sap consisted in cutting the plant into small pieces, freezing first in brine, then in a carbon dioxide ether bath, and finally pressing out the sap as thoroughly as possible through cheesecloth. It is realized that the exact concentration of the sap is dependent upon the technique employed, but the results are comparative and the general magnitudes, which are of interest in this discussion, are probably not far different from those obtainable with other methods of extraction. Osmotic pressures were determined by the freezing point method, conductivity measurements in the usual manner at a temperature of 25° C. The hydrogen ion concentrations were measured with the aid of the hydrogen electrode, using the apparatus described by SHARP and the author (5). The data for the freezing point depressions, conductivity, and hydrogen ion concentration of the various cultures are summarized in table I.

Effect on osmotic pressures

Considering the total osmotic pressures first, it will be noted that both the tops and roots, either in the acid or neutral solutions, reflect the concentration of the nutrient solution, although no very definite relationship is apparent. The highest osmotic pressure is found in the sap from the plants grown in the acid nutrient solution of highest concentration (1.72 atmospheres). The roots of these plants showed marked evidence of injury. In all cases

TABLE I

Osmotic pressure, conductivity, and H ion concentration of plant sap in water, sand, and soil cultures

Total solids approximate p.p.m.	Nutrient solution			Plant sap from tops			Plant sap from roots		
	Osmotic pressure (atmospheres)	Specific resistance (ohms)	H ion concentration P_H	Osmotic pressure (atmospheres)	Specific resistance (ohms)	H ion concentration P_H	Osmotic pressure (atmospheres)	Specific resistance (ohms)	H ion concentration P_H
	Barley plants 8 weeks, grown in water cultures								
200 ...	0.07	3870	5.50	8.01	97	5.68	3.62	125	6.44
200 ...	0.07	3230	6.53	7.55	76	5.68	3.69	137	6.12
1400 ...	0.58	550	5.48	8.13	61	5.85	4.11	117	6.83
1300 ...	0.56	528	6.83	8.35	66	5.82	....	....	....
2300 ...	0.88	347	5.14	8.86	65	5.99	5.04	102	6.97
2200 ...	0.88	347	6.76	10.26	50	5.90	4.52	119	7.08
4500 ...	1.72	196	4.94	11.40	53	5.95	4.90	95	....
4300 ...	1.70	189	6.14	10.24	53	5.90	5.63	77	6.97
	Barley plants 7 weeks, grown in sand cultures								
2500 ...	0.94	335	6.97	10.66	46.9	6.12			
5000 ...	1.81	220	6.97	11.74	42.0	6.15			
8000 ...	2.75	148	6.97	12.24	38.9	6.20			
	Barley plants 6–7 weeks, grown in 6 different soils								
600 ...	0.22*	....	7.03	9.96	59.9	0†			
600 ...	0.21	....	7.15	9.52	60.4	6.12			
900 ...	0.33	....	7.15	10.96	64.2	6.15			
500 ...	0.16	....	7.03	10.14	69.2	0†			
500 ...	0.19	....	7.17	9.97	71.5	5.99			
200 ...	0.08	....	7.34	9.11	65.8	6.12			

* This column represents concentration of soil solution at about time plants were collected; previously the concentration was higher.

† No determination was made.

the osmotic pressure of the tops is much greater than that of the corresponding roots. These findings are in general agreement with those of McCool and Millar. The tops of the plants grown in the various soils have osmotic pressures similar to those found in the water culture experiments. The osmotic pressures of the soil solutions, as determined by the method of Bouyoucos and McCool, varied between 0.08 and 0.33 atmospheres at about this stage of growth of the plant. They are thus quite comparable with the concentrations of certain of the solutions used in the sand and water culture experiments. In every instance the osmotic pressure of the plant sap is much higher than that of the nutrient medium.

All of the samples of plant sap have a very high specific conductivity, and very decided variations are exhibited by the different water cultures. The concentration of the nutrient solution has unquestionably had a pronounced effect on the electrolyte content of the cell sap. A somewhat greater resistance is found in the root sap than in that from the tops. It is to be noted, however, that the variations in conductivity due to the nutrient solution are generally as great for the tops as for the roots, but in either case only a general relationship is apparent. The conductivities of the plant saps from the various soils were very similar in magnitude to those of the plants grown in water culture solutions of 0.5 to 0.9 atmospheres osmotic pressure. The conductivities of the sand culture plants were somewhat greater, but these plants were two weeks younger. In each case the expressed cell sap has a much higher concentration of electrolytes than the surrounding media, the relationship being 50:1 in the case of the most dilute solution. Thus the nutrient media, the root sap, and sap from the tops show three very dissimilar levels of electrolyte concentration. That the simple laws of diffusion are not sufficient to explain the equilibria involved in the plant absorption and metabolism is well recognized, and the data now presented strikingly illustrate this point of view, with reference to the ion content of the plant and its nutrient solution.

H ion concentration of sap

HAAS (3) and TRUOG (7) have shown that the sap of plants quite generally has an H ion concentration distinctly on the acid side. Determinations of H ion concentration were made on the samples of sap obtained as previously described. Table I shows a comparison of the acidity of the sap from plants grown in water cultures of very different concentration and reactions, as well as in sand and soil media.

It is evident that all samples of tops have almost the same P_H value, although the electrical resistances and osmotic pressures may vary widely. It would seem that the reaction is governed by a definite buffer system. In this connection it will be of interest to state that other experiments reported elsewhere have shown that the plant possesses a marked regulatory influence in the selective absorption from the various phosphoric acid anions; that is, either an alkaline or acid nutrient solution has its reaction quickly changed to approximate neutrality.[1]

The measurements of H ion concentrations on the sap from the tops were very definite and constant, but the determinations on the root sap were less satisfactory. An increase in alkalinity was noted during the measurement, possibly due to the reduction of NO_3 and the absence of a sufficient buffer effect. Apparently, however, the sap expressed from the roots has a nearly neutral reaction in several cultures.

Chemical analyses of plant sap

The analyses presented in table II were made on the expressed sap from plants grown in 6 soils of different origin and productivity. The soils were kept at optimum moisture content and under strictly controlled conditions, and 6 or 7 weeks after planting one or two tillers were separated from each of about 20 plants for each soil examined. The sap was obtained by the procedure already described, and then diluted and filtered through a porcelain candle to separate out any suspended material. The analyses were made by the methods described by STEWART (**6**).

The content of the individual ions substantiates the high conductivity measurements on the sap. All ions are present in relatively great concentration, including the NO_3 ion. Some idea of the relation between the composition of the cell sap and soil solution may be gained by comparison with the data for the soil extracts made at about the same time. There is reason to believe that the relation of several important ions is somewhat

[1] Later experiments have indicated that the HCO_3 ion formed is of greatest importance in regulating the reaction of complete nutrient solutions. A solution of KH_2PO_4 alone retains about the same P_H value.

similar in the soil solution and soil extract. As previously shown, the extract may contain several times the quantity of solutes actually found in the soil solution; that is, in the free water of the soil when it contains optimum percentage of water. The magnitudes have been calculated by the methods of BOUYOUCOS and McCOOL. Estimates of the concentration of ions present in the soil solution indicate that invariably the plant sap has a much greater concentration, and in the case of K and PO_4 ions many times greater. It is evident that the relation of the ions to each other is also quite different in the two cases. In the soil solution

TABLE II

ANALYSES OF PLANT SAP AND SOIL EXTRACTS

SOIL NO. AND TEXTURE	P.P.M. OF EXPRESSED SAP					P.P.M. OF 1:5 SOIL EXTRACT†				
	Total nitrogen*	Ca	K	Mg	PO_4	NO_3	Ca	K	Mg	PO_4
Silty clay loam 3	864	680	5540	300	840	90	70	50	20	9
Silty clay loam 5	1030	640	5660	280	1360	70	90	30	20	21
Fine sandy loam 8	1370	920	6130	280	920	60	70	30	20	12
Fine sandy loam 9	820	1040	5240	290	870	30	30	25	10	10
Fine sandy loam 11	680	620	5690	280	1960	50	40	50	15	30
Fine sandy loam 12	940	640	5440	340	1420	30	30	30	10	12

* From 30–50 per cent in form of NO_3 nitrogen.

† Extracts are much more dilute than soil solution, the total concentration of which is shown by table I.

Ca is present in about the same magnitude as K; in the plant sap the concentration of K is from 5 to 10 times that of Ca. The ratio of Ca to Mg is not very dissimilar, Ca exceeding Mg in all samples, both in the plant and soil.

The question has often been discussed whether the plant reflects the composition of the soil. It is the general consensus of opinion that the analysis of the plant ordinarily gives no indication of the deficiencies or fertilizer needs of a soil. This could scarcely be expected, of course, in view of the complex and changing nature of the two systems of the plant and soil. Moreover, analyses of the mature and ripened plant, such as usually have been made, could not possibly give any insight into the relation of the plant to the soil in the period of active growth. It cannot be too strongly emphasized that both the plant and soil are dynamic systems. The soil solution, as previous work in this laboratory has definitely shown, is changing from day to day, and gradually attains a very low concentration at the time when the plant has completed its maximum absorption. Without consideration of these phenomena it would be useless to hope for any clear understanding of soil fertility problems as related to plant requirements.

That some relation must exist between the inorganic elements in the plant and its nutrient solution is apparent from the data obtained in the water culture experiments. Similarly, concentration and composition of the soil solution should affect the absorption by the plant, but here it is very difficult to establish the relationship. For this purpose it would be necessary to appraise not only the concentration of the soil solution at a given time, but its potentiality for renewal. In the work previously referred to an idea of this factor has been obtained by comparing cropped and uncropped soils. The use of this method has made it possible to show some rather definite relations between water extracts of the soils and crop yield, but in the experiment now under consideration the composition of the sap at the given period bears no constant relation to the final yield of the crop, nor to the composition of the water extracts. An exception to this statement may possibly be found in the case of phosphorus, where the concentration of PO_4 in the soil solution is not improbably reflected in the sap. The K and Mg, and to a less extent the Ca, are of approximately the same magnitudes in all samples. While the soils in question varied considerably in their productivity, apparently the average concentrations of the soil solutions were not sufficiently different clearly to influence the concentration of the cell sap.

It does not follow from the foregoing that further study will not indicate a connection between the soil solution and the elements absorbed by the plant. Before the question is decided it will be necessary to examine not only the cell sap, but the total composition and yield, with the strictest control of the soil and study, not of the ripened plant, but the plant in the various stages of active metabolism.

Summary

The expressed sap from barley plants grown in water, sand, and soil cultures under controlled conditions has been examined with the following results:

1. The osmotic pressures in the sand and water cultures are reflected in the cell sap of the tops and roots.

2. The electrical conductivity of the nutrient solution has a marked influence on the conductivity of the sap. This is as marked for the tops as for the roots. The conductivity of the plant sap is from 4 to 50 times greater than that of the nutrient solution.

3. The sap from the tops of all plants grown in sand and soil cultures or water cultures of different concentrations and reactions had almost the same P_H value, approximately 6.0.

4. Samples of sap from plants grown on 6 different soils under the same climatic conditions were analyzed for important elements. In every case the concentration in the sap was found to be very much greater than in the soil solution.

5. The dynamic nature of the relation between the soil solution and the plant is emphasized.

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