BIOELECTRIC FIELDS OF BEAN ROOTS AND THEIR RELATION TO SALT ACCUMULATION

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Summary

The bioelectric field of a bean root growing in a weakly conducting solution is examined. It is estimated by a method which is described, that a total current of about 3×10^{-7} A flows through the external medium due to the bioelectric source, resulting in power dissipation outside the plant of about 10^{-9} W. This is considered in relation to respiratory energy production in the root.

Studies of the pattern of the electric field have been made with various ions in the external medium, and in particular it is shown that K^+ and Na^+ cause significantly different external current paths. Analyses of the concentrations of these ions in root tissue and observation of their absorption using ^{22}Na and ^{42}K lead to the conclusion that sodium enters the root most strongly in a region 8 mm from the apex, whereas the greatest potassium accumulation takes place nearer the apex. These results are shown to be consistent with the electrical observations, the maximum cation entry being at the most negative region of the external medium in each case.

I. Introduction

Observations of characteristic potential differences between points adjacent to a bean root growing in water have been described in previous publications from the Biophysics Laboratory of this Department. It has been shown (Scott, McAulay, and Jeyes 1955) that the normal steady potential of a root growing actively in a weak solution of potassium chloride is most negative in a region close to the root tip with the top of the root most strongly positive. Oscillatory variations with periods of the order of 5 min are found in some cases to be superimposed on this steady background potential pattern (McAulay and Scott 1954; Scott 1957; Jenkinson and Scott 1961).

The purpose of the present paper is to describe the steady pattern in more detail and under a greater variety of conditions. Experimental techniques have been further improved, and a method of determining the electric current density close to the root surface is described. This enables estimates to be made of the total current generated by the root which flows in the external medium and the total electric power dissipated outside the root.

In the past, most investigations of the bioelectric field have been confined to measurements of potential differences. Little attention appears to have been given to the currents and powers associated with bioelectric sources (cf. Crane 1950). Such information is clearly of importance in any consideration of the possible role

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of the bioelectric field in influencing or controlling development of an organ, as has been suggested by Burr (1947) and McAulay, Ford, and Hope (1951). In particular, the energy of the bioelectric source should be considered in relation to other energy-producing and energy-consuming processes within the tissue. It may also be desirable to know the quantity of a particular ion moved from one region to another as a result of bioelectric forces. A knowledge of current paths is also important in cases where the plant's field is being modified by the passage of a current from an external source.

Blinks (1933) has observed that currents of up to 10 μA may be drawn from a single *Halicystis* cell without significantly altering its membrane potential. McAulay, Ford, and Hope (1951) estimated the current and power supplied to an external circuit when two contacts were made on the surface of a turnip hypocotyl or couch grass shoot. They found that the current was of the order of 10^{-8} A (depending of course on the resistance of the external circuit) and the external power dissipation was about 10^{-9} W. It should be pointed out, however, that the technique of measurement through isolated contacts of stagnant salt solution is likely to introduce artefacts (Scott, McAulay, and Jeyes 1955) and part of the current and power measured in the experiments mentioned above may have been due to processes resulting from lack of equilibrium of the contacting system. For example, the energy changes associated with an evaporating liquid contact may be considerably higher than the energy associated with the undisturbed bioelectric source. The experiments described in this paper were designed to provide information about the current and power output of a root which was unaffected by the measuring procedure.

The paper also includes descriptions of investigations of the effect of concentration of the external solution on the strength of the bioelectric field, and the effects of various ions in the external solution. It will be shown that there is a significant difference between the potential patterns for roots immersed in solutions containing sodium ions and those for solutions containing potassium or other cations. This observation suggested an examination of the Na^+ and K^+ content of different regions of the root and the manner in which these ions move in and around the root.

Although much attention has been given to the problem of accumulation of salts by roots, few investigators have concerned themselves with the regions of the root through which these substances are being absorbed. In many cases a young root is treated as if it were a homogeneous absorbing material, although there are obvious differences in structure and function between the meristematic, elongating, and mature tissues, and corresponding variations in ability to accumulate ions are to be expected. Brown and Cartwright (1953) studied the absorption of potassium by isolated segments of maize roots. They concluded that the absorption per unit area is greatest in the segment which was 1·5–3·0 mm from the apex at the time of sectioning. Kramer and Wiebe (1952), Wiebe and Kramer (1954), and Kramer (1956) show that phosphate is absorbed most strongly in the tip region. Steward and Millar (1954) report similar findings for the absorption of caesium by *Narcissus*. Steward, Prevot, and Harrison (1942) in a spectrographic analysis found, for barley roots grown in a solution of rubidium bromide, that the rubidium was most concentrated in the lowest 0·5 cm of the root, falling off gradually towards the root base. Similar findings were claimed for potassium. Epstein and Hagen (1952) and

Epstein and Leggett (1954), using excised barley roots, have studied the interference to the absorption of one cation caused by the presence of other cations, but did not determine where these ions entered the root. No studies of differences between the regions of sodium and potassium accumulation have been made.

Results described in this paper show that sodium and potassium are distributed very differently in root tissue. It is deduced that the regions of entry of the two ions into the root also differ considerably, and this is confirmed in preliminary experiments on the influx of the two ions using radioactive isotopes ^{22}Na and ^{42}K. The relation of these findings to the electrical fields produced by the root in the external medium are discussed and it will be shown that a satisfactory explanation for the difference in the electrical pattern for sodium and potassium media can be advanced.

II. Materials and Methods

In these experiments a long pod strain of the broad bean *Vicia faba* L. was used. Plants were grown with their roots immersed vertically in running tap water at 25°C. After 2 days plants were transferred to the measuring bath at 25°C with the roots immersed vertically to a depth of about 20 mm and the cotyledons above water level. Plants were allowed to equilibrate in the measuring baths for at least 1 hr before measurement commenced, the potential pattern showing no appreciable trend in the next 6 hr. Roots which were not elongating rapidly ($>0{\cdot}5$ mm/hr) were discarded.

The apparatus is in most respects similar to that described previously (Scott, McAulay, and Jeyes 1955) but an important modification has been made to the liquid-filled measuring probes through which electrical connection is made from the bath to the mercury–calomel half-cells. Water is now arranged to flow from the measuring bath along the probe to a point near the half-cell where it drips away to waste. This was found necessary to prevent diffusion out through the probe of KCl from the saturated solution in the half-cell. Such diffusion could contaminate the plant surface immediately adjacent to it with a solution of different composition from that surrounding other parts of the plant. In earlier experiments it was thought sufficient to introduce an agar plug between the half-cell and probe, but the amount of KCl diffusing through the plug has since been shown to introduce a significant error in observation of the normal potential pattern especially for external solutions of very low concentration (less than 10^{-3}N). Back flow of bath liquid along the probes entirely prevents contamination of the bath with salt from the half-cell.

Analyses of the distribution of sodium, potassium, and calcium in the root were made by taking 2-mm segments of about 20 roots. These were weighed and squashed in distilled water, and heated to near boiling point for about 1 hr. The method of extraction probably does not release all the ion in the tissue and some may remain bound in complexes and Donnan phases which can survive the heat treatment. The fraction is not expected to be large, at least for sodium and potassium, although this has not been checked by ashing. A Coleman flame photometer was used for the analyses. Details of the experiment with radioactive sodium and potassium are given in Section IV.

III. Determination of Current and Power

The current di flowing through a small area dA of the plant surface is given by

$$di = -\sigma(\partial V/\partial r)dA,$$

where σ is the conductivity of the external medium, and $(\partial V/\partial r)$ the radial potential gradient in the medium adjacent to the plant surface. Thus the total current leaving the root may be obtained by integrating the above expression for all areas of the root where $(\partial V/\partial r)$ is negative, and the current entering the root is similarly obtained by integration for areas where $(\partial V/\partial r)$ is positive. If the bean and bath are carefully insulated to eliminate leakage paths these two currents should be equal.

If the potential (relative to a distant point in the bath) adjacent to dA is V, the power being dissipated by the current passing through this area is Vdi or $-\sigma V(\partial V/\partial r)dA$. The total power dissipated in the external medium may therefore be obtained by integration of this expression over the entire immersed surface of the root.

Preliminary investigation of the current paths in the surrounding medium by mapping of equipotential surfaces indicated that the pattern was complex and usually changing slowly with time. It was therefore necessary to obtain values of the potential and the radial potential gradient at all points adjacent to the root within a few minutes.

The method employed in the present investigation was to use a pair of liquid-filled probes, the tips of which were arranged radially in relation to the root and separated by a small distance. These could be moved together up and down the root. A third probe of large diameter at a distant point in the bath was used as a reference. Separate half-cells were used for each probe, the reference half-cell being earthed. The electrometer could be switched firstly to give the potential between the probe nearer to the root surface and the reference, and secondly the potential difference between the two movable probes. These measurements were taken quickly for each of the four sides of the root, the plant being rotated about the axis of the root between each set of readings.

Since the probe tips could not be reduced below 0·4 mm in internal diameter without introducing an unduly large resistance in the electrometer input circuit, and the tip separation was about 1·0 mm, the potential difference between them when the nearer probe was just clear of the root surface gave the potential gradient not at the root surface, but at a point about 1·0 mm from it. In order to obtain a value of the density of current through the root surface it was therefore necessary to find how the radial potential gradient changed in going from the root surface to a position 1 mm away. Examination of the fields around typical roots showed that the gradient is approximately inversely proportional to the distance from the root axis over this range of distance. Appropriate corrections to the values of current density were made on this basis.

IV. Results

(*a*) *The Spiral Nature of the Field*

The field lines in the external medium along which the current flows are seldom planar but usually spiral around the root. This is shown from differences in the

observed potential pattern along different sides of the root, indicating that the field has a tangential component. The degree of spiralling may be expressed by a "spiralling factor", which is the ratio of the tangential component of the field to the component in the plane of the root axis. Values of this factor close to the root

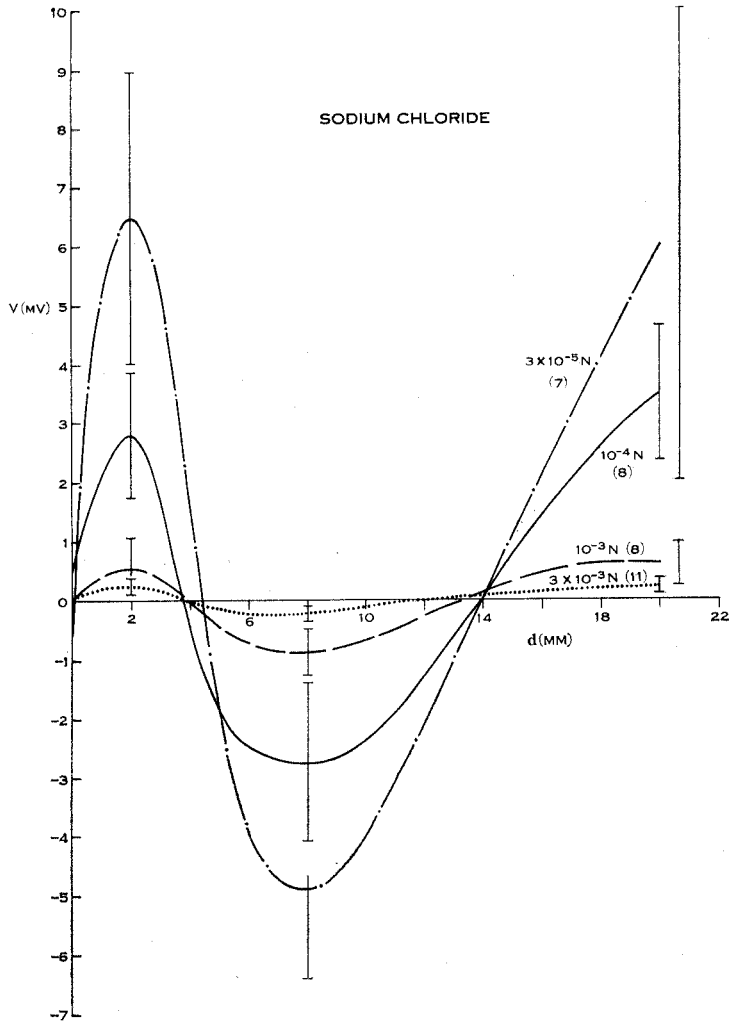

Fig. 1.—Showing the potential V near the root (relative to a distant point in the bath) plotted against distance d from the root tip for roots immersed in four concentrations of sodium chloride. The number of plants in each sample is shown in brackets. The limits are the 95% confidence limits for the mean values.

averaged for 16 plants in 10^{-3}N KCl ranged from a maximum value of 0·34 half-way along the root to 0·15 at about 4 mm from the root tip. No consistent pattern of spiralling was observed (clockwise or anticlockwise) nor was the asymmetry shown

to be related to any obvious biological asymmetry such as bending. The complexities of the spiralling field will not be discussed further in this paper and all observations will relate to the field component in the plane of the root axis.

(b) Effect of Concentration for Roots Immersed in NaCl Solution

A series of experiments has been performed with roots immersed in NaCl solution to test the effect of concentration on the potential pattern. The results are summarized in Figure 1 in which the potential in the bathing solution close to the root surface is plotted against distance from the root tip. The potential is measured

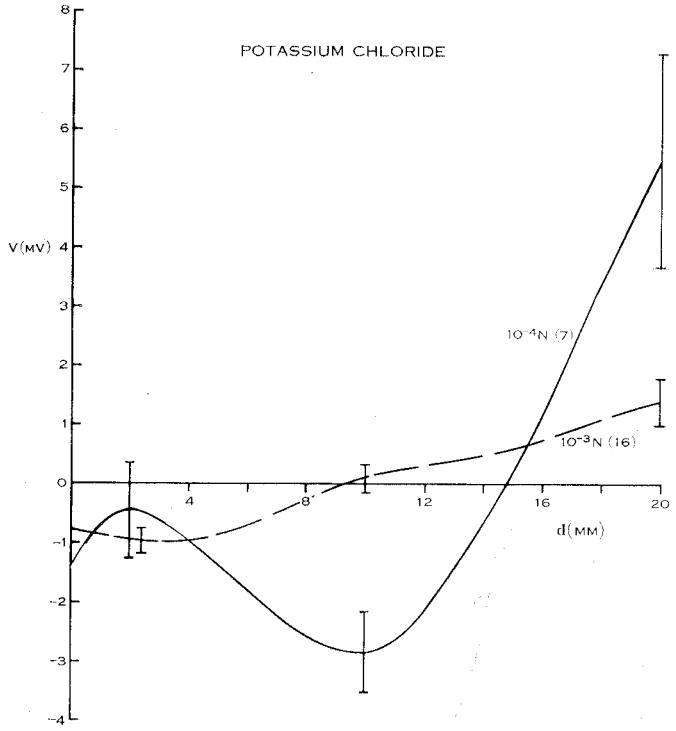

Fig. 2.—Graphs relating V and d for two concentrations of potassium chloride. The number of plants in each sample is shown in brackets.

relative to a distant point in the bath. In these and in all subsequent graphs the limits shown are the 95% confidence limits for the mean value. The range of concentrations used was from 3×10^{-5} to 3×10^{-3}N, a different set of plants being used at each concentration. At weaker concentrations the resistance of the probes was so large that electric pick-up in the input circuit became troublesome, while for stronger concentrations potentials in the external medium nowhere exceeded 0·1 mV.

It is seen that at all concentrations the potential is positive in the basal region of the root and most negative about 8 mm from the root tip. There is a second potential maximum about 2 mm from the root tip. Change to another concentration does not alter the shape of the graph but affects only its scale, the magnitude of the

potentials being, of course, greater in the weaker solutions. Over the range of concentrations used a tenfold concentration change produced a fivefold change in the height of the potential peak near the tip.

(c) *Comparison of the Bioelectric Pattern for Roots in KCl and NaCl*

Figure 2 shows the potential along the root for plants immersed in KCl solutions of concentrations 10^{-3} and 10^{-4}N. In the stronger solution there is no sign of the potential peak in the meristematic region near the root tip that was observed in NaCl. For KCl this region is most negative indicating an inwardly directed current, whereas for NaCl current flows from the root in this region.

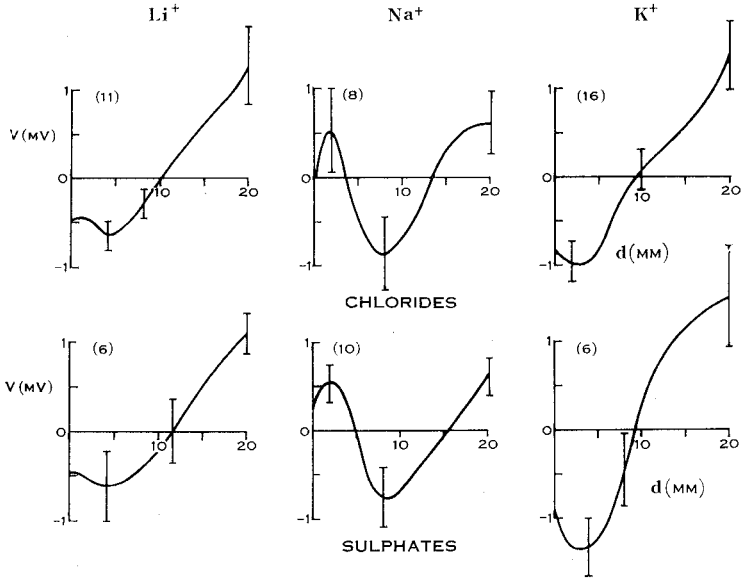

Fig. 3.—Graphs relating V and d for the chlorides and sulphates of lithium, sodium, and potassium. Concentration of each solution = 10^{-3}N. The number of plants in each sample is shown in brackets.

In 10^{-4}N KCl the 2-mm region is significantly less negative than a region half-way up the plant, yet the electric current is still inward. Note that the effect of changes in KCl concentration on the electrical pattern cannot be described in terms of a change in scale as was done for NaCl. Concentration of KCl affects the shape of the potential graph as well as the scale.

A series of roots was measured in a solution containing a mixture of KCl and NaCl, each 5×10^{-4}N. The shape of the potential graph was intermediate between that of the 10^{-3}N KCl graph and the 10^{-3}N NaCl graph. This demonstrated that neither salt exerted a dominant influence on the electrical pattern.

(d) *Effect of the Ionic Medium on the Potential Pattern*

The effects of various bathing solutions containing K^+, Na^+, and Li^+ ions at 10^{-3}N concentration are compared in Figure 3. It is seen that there is no significant

difference between the patterns for the chloride and sulphate of each of the three cations, suggesting that the anion may play an unimportant part in determining the electrical response. This is confirmed in a further series of measurements in sodium glutamate which do not differ significantly from those in other sodium solutions. For the ions of the three alkali metals studied the K^+ and Li^+ patterns are not significantly different. The greatly different pattern for Na^+ is another instance of the remarkable ability of biological systems to distinguish sodium from other alkali metals.

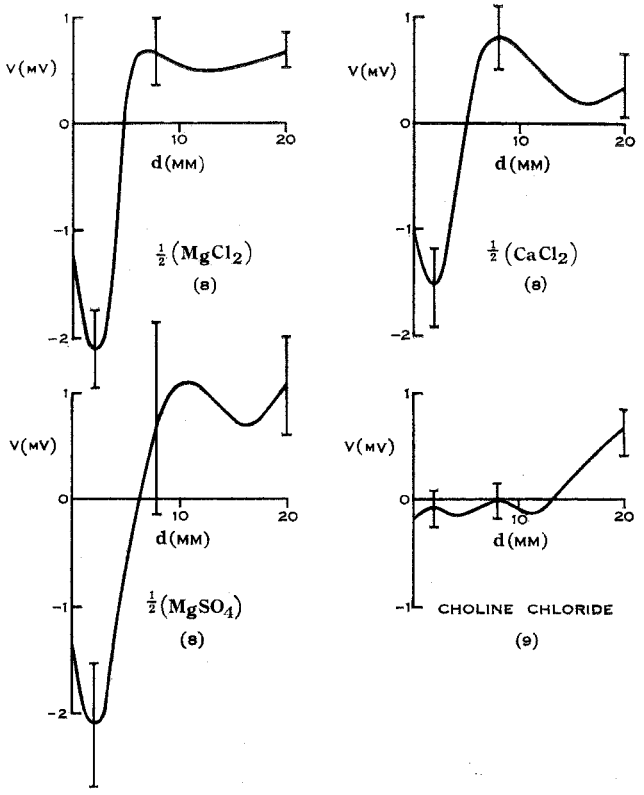

Fig. 4.—Graphs relating V and d for salts of calcium and magnesium, and for choline chloride. Concentration of each solution = 10^{-3}N. The number of plants in each sample is shown in brackets.

Figure 4 shows observations obtained for roots measured in the divalent ions Mg^{2+} and Ca^{2+}. The effect of these cations is to produce a deep negative trough at the meristem, the potential of the upper three-quarters of the root being positive and approximately uniform. Once again the similarity between sulphate and chloride is seen.

A series of measurements in choline chloride solution indicated no significant potential except in the basal region (Fig. 4). The choline ion is assumed not to

penetrate the root tissue in appreciable quantity, and the absence of an electric field in the growing region of the roots confirms that this is related to the absence of penetrable cations.

(e) *Measurements of Current and Power*

Table 1 gives values of the total current leaving the root and returning to it, the maximum current flowing through unit area of the plant surface, and the total power dissipated in the external medium due to the bioelectric current. The measurements have been made for four concentrations of NaCl and two of KCl. The tabulated results were obtained in the manner described in Section III.

TABLE 1

MAGNITUDE OF BIOELECTRIC CURRENTS IN BEAN ROOTS AND OF POWER DISSIPATED IN SODIUM AND POTASSIUM CHLORIDE SOLUTIONS OF VARIOUS CONCENTRATIONS

The limits are the 95% confidence limits for the mean values

No. of Plants	Salt Concn. (equiv/l)	Total Current per Root (A)	Max. Current Density (A. mm^{-2})	Total Power per Root (W)	
				Measured	Estimated
			Sodium Chloride		
11	3×10^{-3}	$3\cdot05\pm0\cdot77\times10^{-7}$	$16\cdot2\pm7\cdot2\times10^{-9}$	$1\cdot7\pm0\cdot9\times10^{-10}$	$1\cdot3\times10^{-10}$
8	10^{-3}	$3\cdot52\pm0\cdot62$	$16\cdot3\pm6\cdot9$	$6\cdot6\pm2\cdot0$	$5\cdot1$
8	10^{-4}	$1\cdot69\pm0\cdot55$	$8\cdot3\pm4\cdot0$	$10\cdot8\pm7\cdot0$	$11\cdot8$
7	3×10^{-5}	$0\cdot73\pm0\cdot16$	$5\cdot3\pm1\cdot1$	$8\cdot8\pm3\cdot1$	$7\cdot3$
			Potassium Chloride		
16	10^{-3}	$4\cdot58\pm0\cdot94$	$9\cdot1\pm5\cdot4$	$10\cdot3\pm3\cdot5$	
7	10^{-4}	$2\cdot04\pm0\cdot35$	$3\cdot6\pm1\cdot5$	$17\cdot0\pm6\cdot7$	

For each root the potential and radial potential gradient close to the surface (the average of measurements on four sides) were found at different distances from the tip. With these values and the diameter of the root the current flowing across the surface of each millimetre length of the root was calculated, and also the power dissipated by this current. These values were plotted against distance from the root tip, and the integration performed by counting of squares.

Small differences were usually found in the estimates of total current leaving the root and total current entering it. Since electrical neutrality requires that these values must be the same (assuming that all leakage paths have been eliminated) differences must have been due to errors of measurement. The values used for Table 1 were the averages of the estimated outflowing and inflowing currents.

The maximum current density was observed to occur near the meristem for NaCl and in the most negative region for KCl. In the case of NaCl the maximum current densities were about four times greater than the average for the whole immersed root surface. The factor was rather less in the case of KCl. Power output, depending on both potential and current differed considerably from plant to plant, and in some cases the confidence limits are seen to be rather large. For solutions

of the same concentration there was no significant difference between KCl and NaCl either for current or power. The total current decreased as the concentration decreased, but the total dissipated power may reach a maximum in the case of NaCl for a concentration of about 10^{-4}N. The significance of this will be discussed later.

(*f*) *Measurements of Concentrations of Ions in Root Tissue*

Figure 5 shows the concentrations of soluble K^+, Na^+, and Ca^{2+} in 2-mm segments of bean roots plotted against distance from the root tip. The concentrations

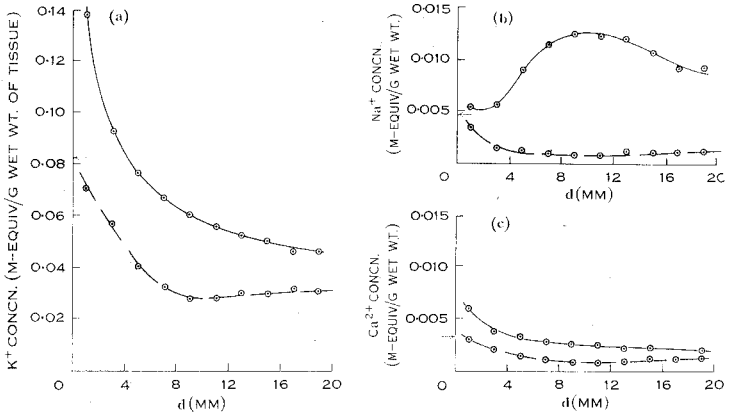

Fig. 5.—The distribution of potassium, sodium, and calcium ions in the root, *d* being the distance from the root tip. The full lines refer to beans grown in tap water enriched with potassium chloride (see text, p. 92) and the broken lines to beans grown in distilled water. The arrows on the ordinates indicate the concentrations of these ions in the bulk tissue of the cotyledons.

are expressed as milliequivalents per gram (wet weight) of tissue. Each graph represents the average of three experiments, about 20 roots being used in each experiment. There were no appreciable differences between the results obtained in the three experiments.

TABLE 2

CONCENTRATIONS OF IONS (IN M-EQUIV/L) IN HOBART TAP WATER

Na^+	K^+	Ca^{2+}	Mg^{2+}	Cl^-	SO_4^{2-}
0·16	0·006	0·18	0·12	0·16	0·03

In one series of experiments (the unbroken lines in Fig. 5) the plants had been grown in running tap water enriched with KCl to make the K^+ concentration about 0·25 mN. Potassium was added because Hobart tap water (Table 2) contains very little of this ion and it was thought desirable to examine the ionic content of roots grown in a medium containing comparable amounts of sodium and potassium.

Roots which had been grown either in the enriched tap water or in ordinary tap water settled down within an hour to produce the typical potassium potential pattern when transferred to a KCl bath for measurement.

The plants were grown for 2 days in this medium, the age being reckoned from the time the seed was set up in the growing bath, having been previously soaked and peeled. At this stage the roots were approximately 25–30 mm long.

It is seen that the concentration distribution of sodium in the root differs markedly from that of potassium or calcium. Potassium and calcium are most concentrated in the tip region, becoming steadily less so as the root base is approached. On the other hand the sodium concentration is least in the tip region and reaches a maximum about 9 mm from the tip where the cells have just ceased elongating. Older cells near the root base have rather less sodium.

Analyses have also been made of the concentrations of these ions in the bulk tissue of the cotyledons. These values are indicated on the graphs. The concentration of potassium is seen to be much higher than that of sodium or calcium.

The broken lines in Figure 5 refer to the concentrations of the same ions for roots which had been grown in plastic containers through which glass-distilled water was flowing. The rate of flow of water was not sufficient to remove all ions leaching from the partly immersed cotyledons, but their concentrations around the roots were not greater than 10% in the case of potassium, and 3% for calcium and sodium, of the corresponding values for the enriched tap water medium. Although the roots were of the same age as those grown in enriched tap water, the average length was less. Only actively elongating roots were used in the experiments. These graphs indicate in each case that the ion is most concentrated in the tip region. The variation of concentration of potassium and calcium along the root is similar to that observed in enriched tap water, although the concentrations are less throughout. In contrast the sodium distribution is very different in the two cases.

It appears that a substantial part of the potassium and calcium in roots of this age is contributed by the cotyledons. For sodium, however, the concentration in all except the root tip is very low unless sodium occurs in the growing medium.

The difference between each pair of graphs is taken to indicate the amount of ion in the root for which the external ionic medium is responsible. The difference exists either because ions are being actively absorbed by the root from the enriched tap water or because less salt is leached from the root in this medium than in distilled water.

(*g*) *Absorption of* ^{42}K *and* ^{22}Na *by the Root*

A single experiment was conducted to observe the active accumulation of sodium and potassium by intact bean roots using the radioactive isotopes ^{22}Na and ^{42}K. In order that the same roots could be used for studies of the simultaneous uptake of potassium and sodium, the medium in which the roots were immersed contained both radioactive ions. The roots were 2 days old and had previously been grown in a medium of approximately the same ionic composition as the radioactive bath. A group of 20 plants was taken from the radioactive bath after a period of

1 hr, and further groups each of six plants after 6 and 20 hr immersion. They were washed for 1 hr in a non-radioactive bath of the same ionic content. This length of time was considered sufficient to remove exchangeable radioactive ions contained in the free spaces of the root (Hope and Stevens 1952) and the remaining radioactivity was assumed to be associated with ions which had been actively accumulated. The plants were then blotted and the roots sectioned into 1·8-mm segments. Groups of corresponding segments were weighed, squashed, dried, and counted using a Phillips end-window counter. The initial count registered both sodium and potassium. A further count after a period of 28 days gave sodium alone since all the short-lived ^{42}K had decayed.

The total (radioactive and non-radioactive) concentrations of potassium and sodium in the external medium were $4 \cdot 9 \times 10^{-3}$ and $9 \cdot 1 \times 10^{-5}$N, respectively. The potassium concentration was relatively high because ^{42}K was not available from

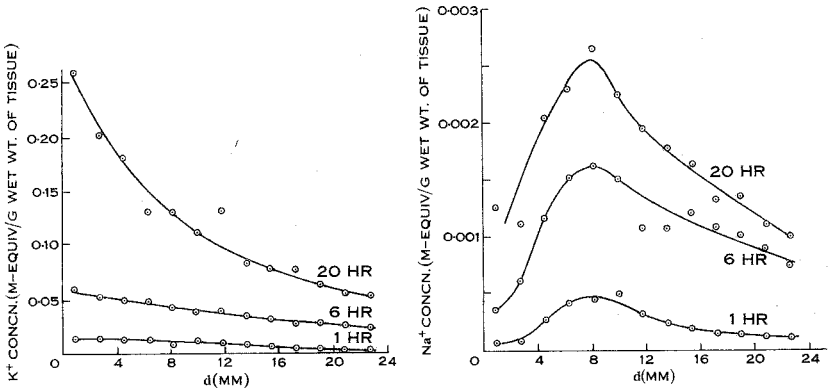

Fig. 6.—Concentration of sodium and potassium (radioactive and non-radioactive) accumulated by bean roots exposed for periods of 1, 6, and 20 hr to a bathing solution containing ^{22}Na and ^{42}K. Concentrations are plotted against distances of the segments from the root tip when the roots were sectioned at the completion of exposure.

Australian sources at the time of the experiment, and a supply obtained from overseas had fallen to a low specific activity before it could be used. The sensitivity of the counting system was found by evaporating a sample of known volume from the bath and counting immediately and after a period of 28 days under the same counting conditions as for tissue. This gave initial calibrations of $6 \cdot 8 \times 10^9$ counts/min per gram total sodium, and $5 \cdot 8 \times 10^7$ counts/min per gram total potassium, corrections to the potassium calibration being necessary at different stages of the experiment because of the rapid decay.

The results of the experiment are given in Figure 6. The graphs show the total amounts of sodium and potassium accumulated by the tissue while in the radioactive bath (per gram wet weight of tissue) as functions of distance from the root tip.

In the graphs for 1 hr, differences in the regions of accumulation are clearly seen. In this time there has been little elongation of the root and it is assumed that

any internal redistribution of radioactive material along the root or leakage back into the external solution may be neglected. Consequently these data may be used to give the influxes of potassium and sodium across the root surface. For sodium the influx per unit area is a maximum at a distance of 8 mm from the tip, being $1{\cdot}5\times10^{-10}$ equiv/mm^2 hr. It is much less in the tip region and in the upper part of the root. The maximum for potassium is $5{\cdot}8\times10^{-9}$ equiv/mm^2 hr at a distance of about 4 mm from the tip, although for this ion there is less variation along the root. The ratio of these fluxes is approximately the same as the ratio of concentrations of the two ions in the external medium.

The interpretation of the other graphs (6 hr and 20 hr) is less straightforward and will be considered in the next section.

V. Discussion

(*a*) *Consideration of the Bioelectric Circuit*

The current generated by the bioelectric source flows in closed circuits which lie partly inside the root and partly in the external medium. The effective resistance of the current circuit in the external medium depends not only on the resistivity of the medium but also on the paths of current flow through it. However, for a root grown in NaCl, it has been shown that the potential pattern is unaffected in form by concentration and this indicates that the current paths in the external medium are also unaffected by concentration. It follows that the effective resistance of the current circuit in the external medium is proportional to the resistivity of the medium, and this is very nearly inversely proportional to the NaCl concentration.

It is therefore possible to test whether the measurements of potential difference, current, and power at different NaCl concentrations are compatible with those expected for a simple model (Fig. 7) in which the bioelectric source is assumed to have constant e.m.f. E and is in series with a constant internal resistance R and an external resistance (r/c), c being the NaCl concentration in the external medium, and r the external resistance at unit concentration.

The following relationships apply to this simple circuit:

$$1/i = R/E + r/cE,$$

and

$$1/v = cR/Er + 1/E,$$

i.e. for this model linear graphs would be found to relate $1/i$ and $1/c$, and $1/v$ and c. Interpreting i as the total current flowing in the external medium and v as the peak to trough potential difference in the external medium, graphs can be plotted to test whether these relationships hold for the bioelectric circuit (Fig. 8). As these graphs are approximately linear over the range of concentration investigated this may be considered to be some justification for the simplifications made in the model and the assumption that E and R are independent of external concentration. Furthermore the characteristics of the graphs permit estimates to be made of the values of E, R, and r. These values are respectively 12·5 mV, 34·4 kΩ, and 4·13 kΩ, the value of r being for a one millimolar solution.

Values of the power dissipated in the external medium as heat can now be calculated from these values of current and effective resistance of the external medium. These values are included in Table 1 and are seen to be in reasonable agreement with the measured values, being a maximum in each case at a concentration of about

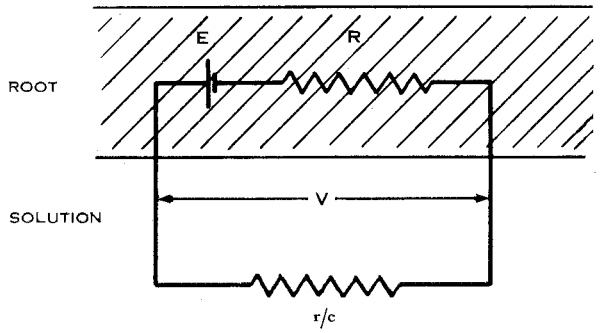

Fig. 7.—Simplified model of the bioelectric circuit (see text, p. 95).

10^{-4}N. This occurs when the effective external resistance is equal to the effective internal resistance. Power is also dissipated within the root due to its internal resistance. The value of this (i^2R) is greater than the power dissipated externally for media of high concentrations and less for media of low concentrations.

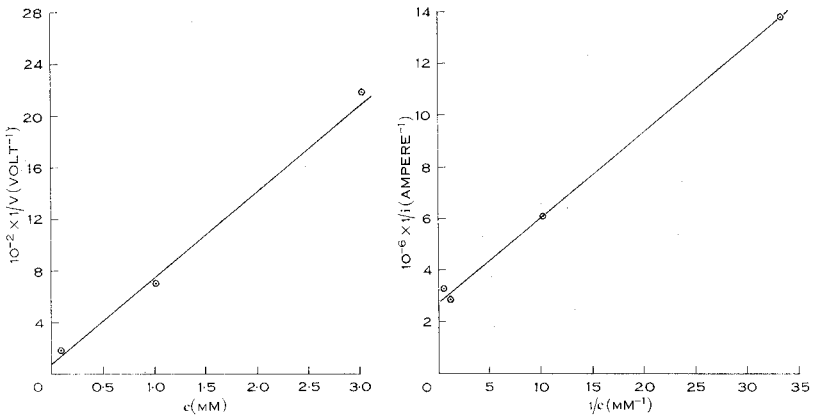

Fig. 8.—Graphs relating $1/v$ and c, and $1/i$ and $1/c$ for bean roots in sodium chloride solution (see text, p. 95).

It would appear from these results that changes in the electrical measurements observed for roots in NaCl are due merely to changes in external resistance when the concentration is changed and not due to substantial changes in the electromotive source or internal resistance. This is not so for KCl for which the pattern of current flow changes with concentration as well as the magnitudes of the electrical measurements. At very low concentrations the KCl pattern may become similar to the NaCl pattern.

(*b*) *Proportion of Metabolic Power Dissipated by the Bioelectric Current*

It is of interest to compare the amount of power dissipated ohmically by the bioelectric current with the total amount being released by respiratory processes within the root.

Doyer (1915) made an estimate of the energy released in respiration by young wheat rootlets based on the amount of CO_2 liberated. He assumed that the CO_2 had arisen from the complete decomposition of starch, according to the equation

$$C_6H_{12}O_6+6O_2 \rightleftharpoons 6CO_2+6H_2O$$
$$\Delta F = -674 \text{ kcal/mol.}$$

On this basis he calculated the total energy released as about 6×10^3 cal . hr^{-1} kg^{-1} which corresponds to a total power of 7×10^{-3} W . g^{-1}. This is an upper limit of power production and would be less if the starch were not completely broken down. He also measured directly the rate of liberation of heat energy by the roots. This was about 3×10^{-3} W . g^{-1}.

If these results are applicable to bean roots, a typical root (20 mm long, 3 mm diam.) would liberate a maximum of 10^{-3} W through respiration, about 4×10^{-4} W of this being in the form of heat.

It has been shown in this paper that the bioelectric current dissipates about $0{\cdot}7\times10^{-9}$ W in an external medium of 10^{-3}N NaCl. An additional amount of about $4{\cdot}2\times10^{-9}$ W is dissipated in the internal current circuit. It is therefore seen that only a few millionths of the total power production of the root are dissipated ohmically by the bioelectric current.

It is, of course, true that electric forces are doing work across membranes of individual cells, and the energies associated with these may be considerable. Studies of large single cells show that these electric forces play an important part in determining the ionic balance of the cell. The comparison made in this section concerns only the macroscopic bioelectric field, an integrated effect of all the cells in the root which causes current to flow through the tissue and the surrounding medium. If it is to play a part in controlling the development of the root it is evident that considerable power amplification is necessary. Sufficient power amplification might be available through the action of plant growth substances (such as β-indolylacetic acid), the movement of very small quantities of which can have a large influence on the plant's development. The possibility that local auxin distribution is affected by the bioelectric current is discussed elsewhere (Jenkinson and Scott 1961).

(*c*) *Ionic Movements in and around the Root*

It has been shown that there are considerable differences in the distributions of potassium and sodium in a root which has been grown in a medium containing these ions. In the case of sodium (Fig. 5, unbroken line) the concentration 8 mm from the tip is much greater than at 3 mm in spite of the rapid enlargement of cells in this region. It is clear that there is considerable influx of sodium into this region of the root. The low sodium concentrations for roots grown in distilled water and the

low sodium content of the cotyledons suggest that very little sodium is obtained by the root from the cotyledons and it would therefore appear to come almost entirely from the external solution. The meristem contains little sodium, and this supports the general belief that sodium is not required for metabolism and the main purpose of the sodium which enters the young root appears to be to fill up vacuolating cells. Mature tissue is found to have less sodium the further it is from the root. This may be due to leakage from the oldest cells to the external medium or losses of sodium from this region to other parts of the plant.

On the other hand, the highest concentration of potassium is in the meristem and there is a gradual fall towards the root base. The cotyledons act as reservoirs of concentrated potassium supplying the lower parts of the root possibly through the vascular system. Brown and Cartwright (1953) maintain that potassium may reach the lower part of the root along procambial strands which are found within 2–3 mm of the apex.

The root obtains additional potassium if this ion is present in the external medium, some apparently entering in the meristem, although substantial amounts are received by the elongating region (3–8 mm from the apex) since there is an eightfold increase in length of cells in this region and less than a twofold decrease in potassium concentration. As with sodium, leakage or translocation may account for the reduced potassium concentration for mature cells furthest from the tip. Calcium distribution is similar to that for potassium.

The deductions on ion movements made from an examination of the bulk concentrations of sodium and potassium in root tissue are supported by the preliminary experiment on absorption of radioactive ions, although it should be made clear that the experiments are not directly comparable as the relative concentrations of cations in the external media are considerably different in the two cases. After immersion for 1 hr in a bath containing ^{42}K and ^{22}Na it has been shown that sodium is actively accumulated most strongly in a region about 8 mm from the tip, with very little uptake in the tip region. Potassium absorption shows less variation along the root but the influx per unit area is a maximum at about 4 mm from the tip.

The graphs for longer periods of immersion in the radioactive medium remain similar in shape to the 1-hr graphs. Care must be taken in interpreting these results. During a period of say 20 hr some meristematic cells will commence to elongate, move further from the root tip, and eventually pass out of the elongating zone as mature cells. At all times during this period they will be absorbing ions at a rate appropriate to their distance from the root tip. (It is assumed that a steady state exists, i.e. that accumulation by cells at a particular distance from the tip is not a function of time.)

If there were no redistribution of ions along the root interior, or no efflux to the external medium, it would be expected that the older tissues would become relatively more concentrated in comparison with younger tissues and the peaks of the concentration graphs would move towards the root base as the time of immersion in the radioactive medium increased. There are several possible reasons why this was not observed in the present experiment:

(1) The root may not have elongated actively during the entire period of immersion in the radioactive bath.

(2) Rapid redistribution may take place within the root leading to greatest concentrations at 8 mm for sodium and at the tip for potassium. A downward translocation of various ions from mature root tissue in barley has been observed by Wiebe and Kramer (1954). This could explain why all three graphs of radioactivity (Fig. 6) and the bulk concentration graph (Fig. 5) are so similar in shape for both potassium and sodium.

(3) There may be a net efflux of sodium and potassium from the basal parts of the root even though there is considerable entry of ^{22}Na and ^{42}K into this region.

Further more carefully controlled experiments are needed to follow the subsequent distribution of ions once they have entered the root.

The ion movements suggested from these experiments are in accord with the observed electrical patterns for roots measured in solutions containing sodium or potassium (Fig. 3). In each case the positively charged ions are approaching the root at a region where the external potential is negative. The external potential for the sodium medium is positive near the apex and here there is practically no sodium accumulation. Any cations leaving the root in the basal region do so where the external potential is positive. If there is a net influx of cation into the root there must be a similar influx of anion to preserve electrical neutrality. In order to explain the observed electrical pattern it is assumed that the anion is absorbed more generally over the root surface. The amount of potassium absorbed in 1 hr by the lower 10 mm of the root can be calculated from the radioactivity data to be about $2{\cdot}5\times10^{-7}$ equivalents. The total current entering this region (for a root in 10^{-3}N KCl) is $4{\cdot}6\times10^{-7}$ A and this would be carried by $1{\cdot}7\times10^{-8}$ equivalents of cations per hour. Thus if the potassium influx exceeds the anion influx by 7% in the lower part of the root, this is sufficient to account for the observed electric current.

The electrical pattern could also be explained if the influx of cation in one region were balanced by an efflux of cation (either the same ion or say H^+) elsewhere along the root. In this case no anion would enter the root from the external solution, the requirements of new tissue being still met from reserves in the cotyledons. The similarity of potential pattern in solutions in which the anion is chloride, sulphate, or glutamate lends some support to this hypothesis.

It is not proposed to discuss in this paper the implications of these results to possible mechanisms of salt accumulation by roots. Since the sites of greatest activity are in different parts of the root for sodium and potassium, separate mechanisms for the active accumulation of these ions appear to be involved, as is suggested by the experiments of Epstein and Hagen (1952).

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