1293

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In-situ root extent measurements by electrical capacitance methods

F. N. Dalton
US *Department of Agriculture, Agricultural Research Service, US Salinity Laboratory, 4500 Glenwood Drive, Riverside CA, 92501, USA*

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Abstract

A conceptual model is presented that provides a rational basis for using plant root capacitance as an in-situ measurement for assessing plant root development. This method is based on measuring the electrical capacitance of an equivalent parallel resistance-capacitance circuit formed by the interface between soil-water and the plant root surface. Nutrient solution studies using tomato *(Lycopersicon esculentum* Mill.) showed a good correlation between plant root capacitance and root mass. Stage of development studies showed plant root capacitance measurements capable of detecting root development rate and suggested the method to be sensitive to root function. Soil water content was shown to have a significant effect on plant root capacitance measurement. The possibility of using this technique to assess relative root function is discussed. Positioning of the plant shoot electrode was shown to also have a significant effect on measurement of plant root capacitance, demonstrating the need for using consistent measurement techniques. The electrical capacitance method shows considerable promise. More research is needed before it can be used routinely.

Introduction

The complexity of in-situ root measurements is staggering especially when the measurement is made in relation to root function such as water and ion uptake. The potential benefits of such a capability are enormous. The ability to make in-situ measurements of plant-shoot properties has advanced our understanding of complex interactions between the micro-climate and a myriad of physical and chemical processes occurring in the shoot. The accessibility of the aboveground parts of plant tissue is an obvious advantage to researchers. Root tissue, however, is relatively inaccessible and the properties of roots growing in a soil under a variety of environmental conditions remain elusive.

In part, this problem has been addressed by the development of the minirhizotron which allows for the in-situ measurement of root length density, (Merrill, 1992; Taylor, 1987; Upchurch and Ritchie, 1984). In addition, there is a need for a dynamic, non-destructive measurement of below-ground growth. Conventional destructive techniques such as root length density obtained from roots washed out of soil samples are inherently labor intensive and inefficient. A non destructive technique for the direct in-situ measurement of active plant root extent, mass and surface area is important not only for studying many plant phenomena related to plant root development, but also for fundamental verification of many root water extraction paradigms. Models of water and ion transport are based on the fluxes of these constituents across active root surfaces. The area across which these fluxes take place for all intents and purposes is unknown. The term "active" in relation to root surface area or extent, is used here to recognize the uncertainties that exist in quantifying, for example, the effective fraction of the total root surface area that is contributing to water and ion transport, mineral nutrition and nitrogen fixation.

Micro scale studies of transport phenomena in root tissue, such as the classic studies of Brower (1953) and Ginsburg (1970) offer no great difficulty because the dimensions of the system are easily measured. However, macro scale studies of entire root systems with respect to water extraction, using the classic analysis of Gardner (1964), present a more difficult problem and have depended on estimates of root length density. Veen (1992) emphasize the importance of root-soil contact on water uptake efficiency using thin section techniques developed by Van Noordwijk(1992). Other transport models for water and ion uptake by plant roots (Barber, 1962; Dalton et al., 1975, 1978), require estimations of an effective root surface area which is facilitating transport. But even a definition of an effective root surface area is elusive and depends on the scale of observation. At the macro scale, root surface area can be considered to be the surface area of a group of right circular cylinders having the same average diameter as the cellular system constituting the roots. At the micro scale, the effective root surface area can be defined to include the surface area of the so-called free space. This surface area encloses a volume defined by the exposed cell walls of a particular cellular packing making up the boundaries of the free space. When modeling water or ion uptake in the soil-plant-air continuum, the gross and poorly defined estimates of the geometrical surface area across which transport takes place become adjustable fitting parameters. For example, root length density measurements used in many models describing root water extraction are without regard to type, age, or size. However, such simplifications are necessary and justifiable when attempting to model such a complex system. The detailed root structure must be approximated to the best of our ability. But even if it is possible to make detailed measurements of root surface area, we are still left with the problem of knowing what proportion of this surface area is significantly contributing to water and ion uptake. Ideally, we seek a measurement that is sensitive to the variable function of the roots making up the root system. What is needed is some physical measurement of a root system which will correlate with root function, for example water and ion uptake, and further, that the measurement integrates over the functional variability that may exist in the root system that cannot be described by traditional root measurements such as root length density. We begin this investigation by first considering possiblities for in-situ measurements that are simply correlated with root properties at the macro scale and that use a powerful new technique which non-destructively gives a measure of plant root extent. The technique applies a previously utilizedelectrical capacitance measurement of plant root systems (Chloupek,l972, 1977; Kendal et al., 1982).

The objective of this paper is to present a conceptual model which gives a rational basis for using electrical capacitance measurements of root systems, and to present techniques and results of such measurements under a variety of experimental conditions with the expectation that it will stimulate a wider interest in the development and use of this method.

Conceptual model

A schematic diagram of the measurement scheme is shown in Figure la. A standard one kilohertz impedance bridge is used for capacitance and resistance measurements between the electrical contacts made at the root crown and a ground electrode inserted in the rooting media. Electrical contact is made with the plant by inserting a small needle electrode into the plant crown. The ground electrode consists of a stainless steel metal rod. Depending upon the application in soil or nutrient solution, the rod can conveniently vary from 10 to 30 cm in length. While the actual current paths in the plant root tissue are not well defined, it is assumed that the most conductive path exists in the ionic solution of the interconnecting xylem tissue. The current paths in soil and culture solution external to the plant root are more well defined. In soil, the current path follows the same path that water would follow if a hydraulic gradient is in the same direction as the electrical field gradient and the conductivity will vary depending on the water content and ionic concentration (Mualem and Friedman, 1991). In culture solutions the conductivity remains relatively constant. An electrical equivalent of this network is shown in Figure 1 b where electrode contact resistances and capacitances are assumed to be negligible and constant. The xylem and/or the phloem tissue form a common electrical conduit as illustrated by the schematic of a simply branched root system. This low resistance and common electical path is separated from the nutrient solution by plant root tissue. The nutrient solution forms a second low resistance and common electical path. The components of this root network can be reduced further to an equivalent electrical network, as shown in Figure lc, where each root segment is numbered (i) and is shown to be represented by a parallel resistance, R_i,- capacitance, C_i, circuit. The grounding symbols represent the common electrically conductive medium of the nutrient solution surrounding the root tissue. This schematic can be unfolded further and is shown in Figure 1d. This represents a simple root system of

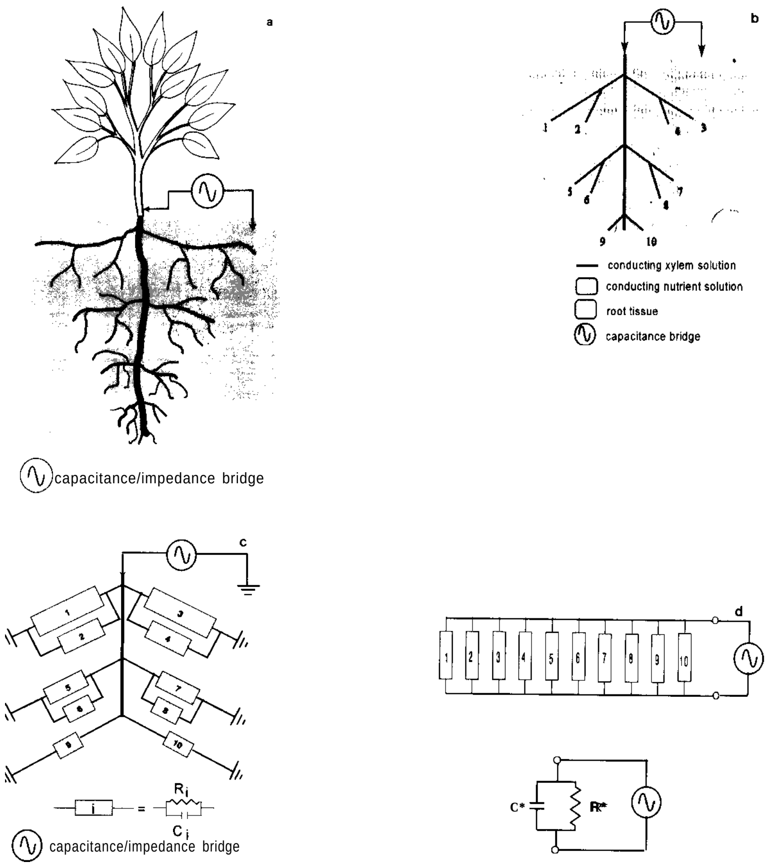

Fig. 1. a: Schematic for plant root capacitance measurement. b: Electrical equivalent diagram of plant root tissue separating xylem solution from nutrient solution, c: Equivalent electrical network of root system of order 10. Each element *(i)* consists of a parallel, R_i-C_i, circuit. d: Equivalent circuit for root system shown in Figure 1c (top) and its equivalent circuit in terms of C* and R* (bottom).

order 10, Figure 1b, but can be generalized to a root system of any order, n.

A measurement of the effective resistance and capacitance of this circuit is given in terms of its equivalent capacitance, C*, and equivalent resistance, R*, where,

$$C^* = \sum_{i=1}^{10} C_i \tag{1}$$

and

$$\frac{1}{R^*} = \sum_{i=1}^{10} \frac{1}{R_i} \tag{2}$$

In this paper we are particularly interested in the effective capacitance of the root system because from Equation 1 it is seen that the effective capacitance is additive with respect to each root element and has the possibility of also being linear, whereas the effective resistance, Equation 2, varies hyperbolically with increasing root elements.

The capacitance of each root element can be modeled according to an axially symmetric cylindrical condenser. That is, if the root tissue of element i has a length L, and dielectric constant, ξ_i, and there is an inner cylindrical conductive element having an effective radius r_{i1} (xylem) separated by root tissue whose outer surface is in contact with an exterior conductor (nutrient solution) at an effective radius r_{i2}, then the capacitance is given as,

$$\mathbf{C} = \frac{\epsilon_i A_i}{4\pi r_{i2} \ln[\frac{r_{i2}}{r_{i1}}]} \tag{3}$$

where A_i is the macro-scale geometrical surface area defined by $2\pi r_{i2}$L. The root surface area of each element is seen to be directly proportional to the capacitaince and also to be dependent on variable geometrical properties. From Equations 1 and 3, the effective root

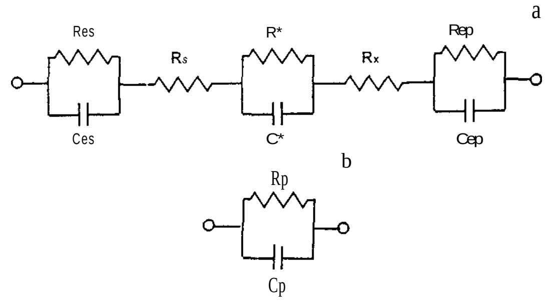

Fig. 2. ***a:*** Equivalent circuit for plant root capacitance measurement. R_{es}-C_{es} are resistance-capacitance of electrode-soil water contact; R_s is resistance of rooting medium; R^*-C^* are equivalent resistance-capacitance of root tissue; R_x is resistance of xylem tissue; R_{ep}-C_{ep} are resistance capacitance of electrode-shoot contact. **b:** Equivalent circuit of Figure 2a whose elements, R_p-C_p, are measured by a capacitance bridge.

capacitance, C^*, becomes

$$C^* = \sum_{i=1}^{n} \frac{\epsilon_i A_i}{4\pi r_{i2} \ln[\frac{r_{i2}}{r_{i1}}]} \qquad (4)$$

In the limit as r_{i1} approaches r_{i2}, and using a Taylor series expansion of $ln[r_{i2}/r_{i1}]$, Eq. 4 reduces to a form describing the capacitance of a set of parallel plate condensers with areas A_i and separation $d_i = r_{i2} - r_{i1}$,

$$C^* = \sum_{i=1}^{n} \frac{\epsilon_i A_i}{4\pi d_i} \qquad (5)$$

To within the narrow limits of the model, Equations 4 and 5 show a correspondence between total root surface area, variable dielectric constants and geometrical factors. It can be envisioned that the unknown variable parameters may behave in a conservative manner and scale with the root size in such a way as to remain fairly uniform. The real behavior of this relationship remains to be shown experimentally, keeping in mind that this simple model in no way addresses the unknown current paths or unknown geometrical configurations making up the surface area contributing to the root capacitance. Within these uncertainties lies the possibility of a measurement that integrates the variable parameters in such a way as to correlate with root surface area or, more importantly, with a measure of root function. Electrical capacitaince measurements have already been correlated with environmental conditions, e.g. hypoxia, anoxia, (Dvorak et al., 1981), and investigations have also been conducted on the electrical impedance of plant tissue as a method of evaluating freeze injury, (Zhang and Willison, 1992).

In addition to the equivalent circuits of the plant root system, the measurement includes other equivalent resistance-capacitance circuits which involve the electrode contacts and the medium resistances. The electrical circuit for the measurement scheme is shown in Figure 2a. This electrical circuit shows the electrode-soil solution interface, $\bar{R}_{es}C_{es}$, the root medium resistance, R_s, the plant root system as shown in Figure Id, R^*-C^*, the resistance of the current path in the xylem solution, R,, and the electrode-plant interface, R_{ep} - C_{ep}. The capacitance measurement made with any impedance bridge actually represents the effective capacitance of the entire circuit. It is interpreted in terms of another simplified equivalent circuit, R_p-C_p, shown in Figure 2b. It is the capacitance C_p that is correlated with variations in plant root extent.

Root systems are hierarchical structures in which bio-mass tends to be relatively more associated with axial members while greater functionality is associated with lateral roots. Among lateral roots, the greatest activity is commonly believed to be associated with higher branching order. Root capacitance is assumed to be more a measure of active root area, and in general, root extent. It is realized that, in general, root mass is directly related to surface area only for a constant diameter root system having a constant tissue density. Root mass is much easier to measure than root length or area and is being used as a necessary experimental expedient. In nutrient solutions studies it is observed that root diameter is relatively uniform and in such a system the above assumption is not too unrealistic.

Applications

Nutrient solution studies

Greenhouse studies

Under the assumption that, to a first approximation, plant root surface area is directly proportional to plant root mass, one can use hydroponics to easily assess the technique of measuring the root system by electrical capacitance methods. While it is realized that this assumption is in general inaccurate, it is reasonable to expect that, for a given cultivar, the relation between root mass and root surface area is approximately linear. In nutrient solution studies, root harvests are simple and plant capacitance measurements are easily correlated with root mass. Therefore, in order to obtain absolute correlations between plant root capacitance and root mass, measurements were made on tomato plants grown in nutrient solutions to test salt toler-

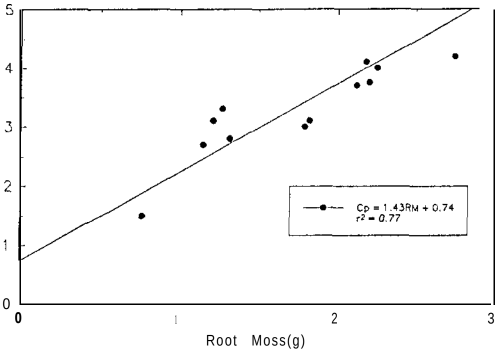

Fig. 3. Root capacitance of three tomato cultivars vs. root mass.

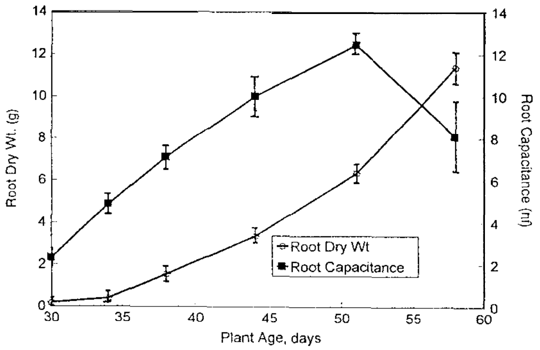

Fig. 4. Root capacitance and dry weight of roots at 37,4 1,44,5 1, and 57 days of age.

ance differences between three cultivars of tomato: Heinz 1350, Walter, and VF 36. A General Radio' impedance bridge was used to make measurements on eight-week-old, twice replicated samples (two plants from each replicate) for each of the four salinity treatments (control, 50, 100, 150 mM NaCl, $CaCl_2$, 5:1 mM ratio). Root growth is decreased with each treatment of increasing salinity thereby providing a variation of root sizes in the plant population under study. Composites were made for each replication and for each cultivar.

The plant electrode used in these experiments consisted of a 28 gauge stainless steel hypodermic needle. The electrode was inserted through the center of the plant stem as close to the most proximal lateral roots as possible. [1] After each measurement, the roots were harvested and dry weight determined. Figure 3 shows composite results of root capacitance measurements for all three cultivars. A linear regression with root mass (dry weight) gives a correlation coefficient of $R^2 = 0.77$. This compares favorably with results obtained using minirhizotron technology, (Merrill et al., 1987; Upchurch, 1985). There are not enough data to explain any of the observed variability in terms of a cultivar dependence of the measurement nor can we be certain that the salt treatments do not change the dielectric properties of the root tissue. A cultivar dependence might be expected if there were differences in the dielectric properties of the root tissues. As with many physical measurements that are not able to give absolute values, the measurement is still useful when investigating relative differences. If in fact there is a cultivar dependence, this information might be exploited and correlated with physical transport properties of the root system. The question of a cultivar dependence will require further study.

Stage of development study

In the above study, plant root capacitance measurements were correlated with root mass of established plants where root size differences were caused by different salinity treatments and the measurements were all made at the same plant age. In order to determine if an in-situ measurement of plant root capacitance can detect differences in root extent due to growth, the relationship between root capacitance and the time course of root development was investigated.

At experimental day zero, 30 one-week-old tomato seedlings (VF 36 Hybrid) were transplanted from the germination beds into 2 L containers filled with a modified half-Hoagland nutrient solution. Root development was monitored with six harvests on experiment days 30, 34, 37,44, 51, and 57. Prior to harvest on each of these dates, five plants were measured for root capacitance. After each measurement, the roots and shoots were separated, dried at 60°C and weighed. The average plant root capacitance and root dry weight of each replication are plotted as functions of plant age for the six different harvest times in Figure 4. The root development rate, shows a normal exponential increase with time. The time course measurement of root capactiance from day 30 reveals the changes in root growth and shows a slight curvilinear response which increases to day 51 and then, curiously, decreases sharply with plant age. It can also be noted that while the root biomass development is continually accelerating with time (concave up) the electrophysical property of the plant root system that confer a value of root capacitance is continually increasing to a maximum but at a decreasing rate (concave down). The

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[1] Names and products are mentioned for the benefit of the reader and do not imply indorsement or preferential treatment by the USDA.

sudden decrease in capacitance past day 51 must be explained on the basis of an effectively reduced active root mass. The root population has reached an age level where suberization, reduced activity or death may so alter the current paths and dielectric properties as to be reflected in a reduced measurement of plant root capacitance. These results may also reflect an inappropriate assumption about the linear proportion of root biomass to root surface area. These measurements made at various stages of growth may represent not only changes in plant root surface area but may include the effects of changes in the electrical properties of maturing root populations. In any case, these observations illustrate the potential of this in-situ measurement for discerning root activity or functionality which is to be distinguished from a macro-scale measure of root surface area. The possibility of distinguishing between root functionality and a macro scale measure of root surface area is an important consideration which could prove to be extremely useful in studying rooting efficiency under various environmental stresses.

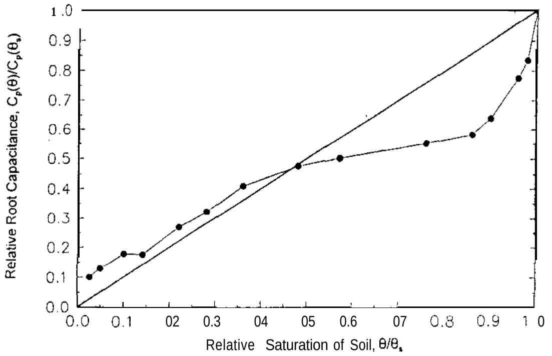

Fig. 5. Relative root capacitance of tomato vs. relative saturation of fine sand.

Dependence of plant root capacitance measurements on soil water content

Figure lb and lc show the entire root surface in contact with the nutrient solution. Since the nutrient solution provides the common external current path for the root capacitance measurement, a reduction in soil water content will result in a reduction of root tissue in contact with the nutrient solution and, therefore, a reduction in the root surface contributing to the root capacitance. This phenomenon was investigated using a well developed tomato plant growing in a fine sand contained in a plastic PVC column 35 cm in height and 12 cm in diameter. Water loss from the rooting medium was limited to that caused by transpiration. Transpiration demand was sufficient to reduce the soil water content to the wilting point during an eight hour time period durning which changes in root mass due to growth could be considered negligible. After bringing the rooting media to saturation, an initial measurement of the plant root capacitance was made. Subsequent measurements were made during the course of water depletion caused by transpiration.

Let $C(\theta_s)$ represent the initial root capacitance measurement at saturation when 100% of the root mass is in contact with the nutrient solution. Let $C(\theta)$ represent the plant root capacitance measurements made at soil water content, θ. The water content dependency of plant root capacitance can be demonstrated with a dimensionless plot of the relative root capacitance, $C(\theta)/C(\theta_s)$, as a function of relative saturation, θ/θ_s. Figure 5 shows that the relative capacitance varies distinctively over three regions of relative saturation. 1) A region of relative saturation between 1 and 0.85 where a steep decline in relative capacitance occurs with only a small1 decrease in relative saturation. The relative capacitance decreases from 1 to 0.58 as the relative saturation decreases from 1 to 0.85; 2) a region of relative saturation between 0.85 and 0.35 where there is only a slight decrease in relative capacitance; 3) a region of relative saturation between 0.35 and, at least, 0.15 where there is nearly a one to one relationship between relative root capacitance and relative saturation.

It becomes immediately apparent that in-situ measurements of plant root capacitance made in the field will have to take into account the effect of soil water content. However, the author has applied this in-situ measurement with success on field grown corn growing in a peat soil by taking measurements immediately following irrigation. It is to be noted that the measurement was repeatable and extremely precise (FN Dalton, unpubl. data). Even though the root capacitance measurement strongly depends on soil water content, relative differences between root development under various environmental conditions could be obtained by taking measurements at some known constant water content, preferably in region 2 where the water content effects are minimal.

Under some conditions, for example when the root size distribution is nearly uniform, it may be possible to interpret the relative capacitance measurement as the fraction of total root surface area in contact with soil water. The possibility also exists that this measurement is better correlated with root function rather than a macroscopic measure of root surface area. An important example of root function is the ability of the root system to extract soil water. All root water uptake models share the same tacit assumption that water extraction is a hydraulic process and that all of the water enters the root in the liquid phase even though the possibility of vapor flux absorption at the root surface was experimentally determined by Dalton (1988). Because of root shrinkage and soil water depletion due to transpiration and drainage, air spaces are created in the root zone and portions of the root surface lose contact with liquid phase water, (Herkelrath et al., 1977; Huck et al., 1970). The fraction of root surface that is in contact with soil water can be of fundamental importance. This fraction has been estimated by Herkelrath et al. (1977) by equating it with the relative saturation of the soil, θ/θ_s. This tacitly assumes that root function with respect to water uptake is equally distributed over the entire root system. In a non-homogeneous root system and with respect to root capacitance, Equations 4 and 5 indicate that the smaller diameter roots (which may have greater functionality) are more heavily weighted with respect to their contribution to root capacitance as long as the dielectric constant of the root tissue remains constant. If it is possible to interpret the relative root capacitance as a measure of the fraction of active root elements capable of water extraction, it is of interest to compare the observed dependency of relative root capacitance on relative saturation with the linear 1: 1 relations used by Herkelrath et al. (1977). The 1:l relationship shown in Figure 5 is approximately duplicated only at a relative saturation less that 0.5. The greatest loss of root function occurs early when the capillary pores first empty. This interpretation of course assumes that the dielectric property of the roots does not change during the course of the measurement. Chloupek (1977) noted a slow increase in the root capacitance of a red clover after the herbage had been removed. Although it is was offered that the cause could be due to an increase in root volume, no information was given as to the water status of the plant, transpiration rate or soil water content. An increase in plant root capacitance with an expanding root volume is consistant with the idea of a greater fraction of the root surface area coming into contact with soil water. While the effect of the root water status on the dielectric property of the root is an important consideration, it is worthwhile recalling that the capacitance measurement is the result of both geometrical and dielectric properties. The relevant question with regard to the initial decline of the relative root capacitance shown in Figure 5 is whether or not this is due to changes in the dielectric properties of the root or to a reduction in the fraction of root surface being measured. As the measurements where made roughly at 30 minute intervals, the time response from saturation can be seen to be quite rapid. From a representative water retention curve for a fine sand, (Baver, 1940) it is estimated that this initial decline takes place where the pore water potential is only - 1 kPa. Under this slight tension and because of the conservative nature of the dielectric properties of materials, it is reasonable to assume that the primary variation is that due to a change in surface area being measured. Even at a relative saturation of 0.85, which delimits the first stage response, the pore water potential is only of the order of magnitude of 10 kPa, where it is reasonable to expect that there is minimal, if any, change in the dielectric property of the root material relative to the large decrease in root surface in contact with the soil water. Under more severe water stress, at tensions greater than 100 kPa where the effect of root water status might be more pronounced, the relative root capacitance follows more closely the 1: 1 dependence. From Equation 5 we can estimate the sensitivity of plant root capacitance to changes in the thickness of the cell tissue by taking the first derivative with respect to that variable. The sensitivity varies inversely with the square of the tissue thickness and since it is always much less than one, small decreases in this dimension due to water stress would cause a relatively large increase in the capacitance measurement. The sensitivity with respect to the dielectric constant and surface area are of the same order of magnitude. The precise role of the effect of the root water status on the dielectric property of the root needs to be clarified. It is unclear at this time rather or not the relative capacitance with respect to relative saturation can be interpreted as a macroscopic measure of the fraction of root surface in liquid phase contact with the soil water or if it will be better correlated with relative root function, e.g. root water extraction. In either case, these innovative possibilities warrant further research.

Plant root capacitance measurement as affected by position of shoot electrode

In the previous experiments, the plant shoot electrode was positioned in the shoot crown as close to the primary lateral roots as possible. The extent to which variations in the positioning of the shoot electrode affect the plant root capacitance measurement is unknown. The plant root capacitance dependence on the placement of the shoot electrode was investigated using a bean plant

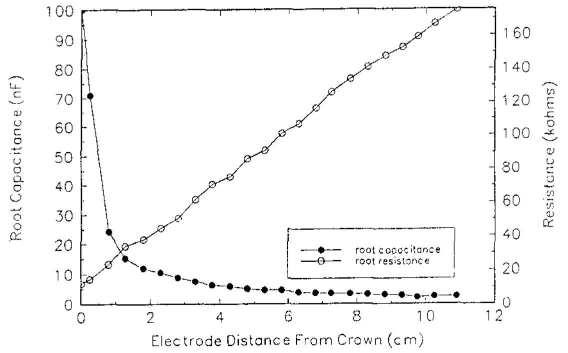

Fig. 6. Equivalent root capacitance and resistance as a function of the distance from crown to electrode placement.

grown in aerated nutrient solution. The roots were fully submerged in the nutrient solution while capacitance and resistance measurements were made after the plant electrode was inserted at various distances above the crown to a maximum distance of 11 cm. The results, shown in Figure 6, show a significant effect of the electrode position on root capacitance measurement and clearly demonstrate the need for careful and consistent electrode insertion procedure. The two distinct trends that the electrode position has on resistance and capacitance measurements can also be used to interpret the effective equivalent circuit of the shoot tissue above the crown. The linear increase in resistance and the hyperbolic decrease in capacitance as the shoot electrode is inserted at increasing distances above the crown suggest that the equivalent circuit of the shoot tissue can be represented by a continuum of capacitance-resistance elements in series as contrasted with the parallel network of the root. In a series configuration, the effective resistance will increase as more shoot tissue is included in the measurement while the effective capacitance will decrease. The primary importance of these results, however, is the recognition that the electrode placement has a significant effect on the plant root capacitance measurement and that shoot electrode contact should be made with consistancy as near the first proximal lateral root as possible.

Conclusions

The measurement of plant root capacitance is shown to provide an assessment of plant root development. The advantages of this method over conventional soil core methods are that the capacitance measurements are in-situ, nondestructive and are not labor intensive. This investigation showed:

1. A good correlation exists between plant root capacitance and root mass of hydroponically grown tomato (r^2 =.77). This correlation compares favorably with those reported for field measurements of root length density using minirhizotron techniques.
2. A time course study of root development and root capacitance measurement showed the ability of this technique to detect root growth. As the root population aged, the measurements showed a decrease in active roots. The measured decrease is thought to be caused by a reduction in root activity due to suberization, reduced activity and death.
3. A strong dependence of the measurement on soil water content was observed. The technique offers the possibility of assessing the traction of soil water in contact with root surface and provides important considerations of root funtion with respect to soil water extraction.
4. Finally, the sensitivity of the measurement to the placement of the plant shoot electrode is shown to be potentially significant. The necessity of a consistent technique for inserting the plant electrode is demonstrated.

More research is required before this technique can be used routinely but, even without an absolute calibration, this method should be considered as an adjunct to other in-situ measuring techniques. Applications for the relative measurements of root extent are numerous and should present many opportunities for use of this technique. Further improvement with this method can be expected with refinements in the plant shoot electrode and when the details of the equivalent circuit and current paths are more fully understood.

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