The organization of roots of dicotyledonous plants and the positions of control points

Thomas L. Rost

Department of Plant Biology, University of California, Davis, CA 95616, USA
*E-mail tlrost@ucdavis.edu

Reviewed: 18 August 2010 Returned for revision: 8 September 2010 Accepted: 21 October 2010 Published electronically: 29 November 2010

Scope and Conclusions

This short paper outlines the types of RAM, i.e. basic-open, intermediate-open and closed, and how they are similar and different, and makes the point that the structure and shape of the RAM are not static, but changes in shape, size and organization occur depending on root growth rate and development stage. RAMs with a closed organization lose their outer root cap layers in sheets of dead cells, while those with an open organization release living border cells from the outer surfaces of the root cap. This observation suggests a possible difference in the mechanisms whereby roots with different RAM types communicate with soil-borne micro-organisms. The root body is organized in cylinders, sectors (xylem and phloem in the vascular cylinder), cell files, packets and modules, and individual cells. The differentiation in these root development units is regulated at control points where genetic regulation is needed, and the location of these tissue-specific control points can be modulated as a function of root growth rate. In Arabidopsis thaliana the epidermis and peripheral root cap develop through a highly regulated series of steps starting with a periclinical division of an initial cell, the root cap/protoderm (RCP) initial. The derivative cells from the RCP initial divide into two cells, the inner cell divides again to renew the RCP and the other cell divides through four cycles to form 16 epidermal cells in a packet; the outer cell divides through four cycles to form the 16 cells making up the peripheral root cap packet. Together, the epidermal packet and the peripheral root cap packet make up a module of cells which are clonally related.

Key words: Root apical meristem, RAM, cell cycle, differentiation, peripheral root cap, closed RAM organization, open RAM organization, epidermis, module, determination, levels of organization, plasmodesmata, T-division, root cap/protoderm initial, columella initial.

INTRODUCTION

Root tips of dicotyledonous plants have been studied for well over a hundred years, with many papers published on root apical meristem (RAM) organization and many other aspects of root structure and development (Popham, 1966; Groot and Rost, 2001a, b; Groot et al., 2003; Heimsch and Seago, 2008). Despite this attention, plant biologists tend to disagree on many fundamentals of the structural organization of roots and the terminology used to describe them. In this short essay, I intend to step away from these controversies and instead discuss observations on some aspects of root structure made primarily in my laboratory over a 40 year period. I would not be so bold as to state that every generalization I intend to make will prove to be law in the long run, but the real intention is to point out control points in the tissues of a root tip where differentiation decisions are made and where molecular biologists need to focus their attention in determining the locations of genetic action and how these decision points are affected by such things as the root growth rate. Before continuing, I need to acknowledge the work of the undergraduate and graduate students, post-doctoral scholars and collaborators with whom I have worked, and many of their published studies will be referenced in what follows.

One reason for the apparent lack of agreement on root structural issues is that the organization and cellular patterns within a root are constantly in flux during root development. As will be pointed out, the organization of the RAM changes during the root growth cycle, and also roots are remarkably responsive to their environment and consequently keep changing (Rost and Baum, 1988; De Tullio et al., 2010). Researchers who fail to take this into consideration will sometimes jump to different conclusions on structural issues when what they are actually seeing is a change in structure due to the responsiveness of the root to its environment. Is it possible to describe a normal condition for anything inside a root? I think it is, but it is important to consider carefully and describe growth conditions and the root growth cycle stage and timing.

What should we know about differentiation control points in the context of complex root tissues? One obvious place to start
is the organization of the RAM. How is the RAM organized? Is it static during root development? Is it the same in all plant families? Does the RAM organization pattern have a function? Relative to the body of the root, are there control points where developmental decisions are made that regulate differentiation events? Is the location of these control points static during root development? What controls the spatial relationship between differentiation events? Finally, relative to cell cycle events, how is the location of cell cycle events regulated? How is the plane of division controlled? Is there a mechanism to ‘count’ the number of divisions within a cell file and cell module? Some of these questions will be addressed in the following from the perspective of where the control points are, but not from the perspective of defining the genetic or hormonal control of those control points; that is left for the new scientists to discover. I will start with the RAM.

ROOT APICAL MERISTEM ORGANIZATION

Many papers on RAM organization have been published, going back to the 1800s (Hanstein, 1870; Janczewski, 1874) and forward to more recent papers by Clowes (1981), Groot et al. (2003) and Heimsch and Seago (2008). Some analyses have simplified patterns and others have plotted many complicated schemes with types and sub-types (Popham, 1966), and in the exhaustive study by Heimsch and Seago (2008) 15 different types of RAM organization were identified. The scheme I will describe is possibly overly simplified but was used in the phylogenetic comparison study by Groot et al. (2003). One thing to note, however, is that in some families of plants more than one RAM organization type may exist (Heimsch and Seago, 2008), so this analysis or any other must be considered tentative and open for additional analysis. In the scheme of Groot et al. (2003) there are three types of RAM – closed (Fig. 1A), intermediate-open (Fig. 1B) and basic-open (Fig. 1C). In their study they compared the RAM organization of representatives from many different families and plotted their RAM type based on the DNA sequence phylogeny data analysis of Solis et al. (2000). This suggested that the intermediate-open type of RAM organization was ancestral, the basic-open type, which is found only in two families, Fabaceae and Cucurbitaceae, is derived and the closed type is advanced. Although these results should be considered open for further analysis, the point being made here is that there are specific types of RAM organization that appear throughout dicotyledonous plant taxa and that generating these different types will require taxon-specific cell cycle and differentiation regulation. The fundamental differences between the types are as follows.

(1) Closed RAM organization. In this type, there are three specific tiers of initial cells (stem cells) from which all other cells in the root body and cap are connected by lineage. One tier for the vascular cylinder, one for the cortex and the other for the epidermis and root cap (flax; Fig. 1A). A fourth tier of initials called the ‘calyptrogen’ derives only the root cap, is found only in grasses and is lacking in roots of dicotyledonous plants.

(2) Intermediate-open organization. In this type, examination of the zone at the boundary of the root cap and body shows some level of organization, particularly for the epidermis/root cap lineage, but the clear and specific identity of the initial tiers is lacking (carrot; Fig. 1B).

(3) Basic-open organization. In this type, the identity of cell files cannot be clonally predicted and instead a zone of seemingly disorganized initials replaces a zone of distinct initials (pea, Fig. 1C).

The next question is, ‘Does the RAM organization pattern remain constant throughout the growth cycle of a root?’ To examine this question, we need first of all to look at the growth cycle of a root; in this case we will use the primary root of a seedling as the model. In studies of the primary root growth cycle of pea (Rost and Baum, 1988; Gladish and Rost, 1993), cotton (Reinhardt and Rost, 1995), Arabidopsis (Zhu et al., 1998a, b) and five other species (Chapman et al., 2003) a similar four-step pattern has been observed.
(Fig. 2). Immediately after emergence the primary root shows an accelerated growth rate, followed by a period of relatively constant growth, then a deceleration and finally the primary root ceases elongation at a determinate length. The precise determinate length is a function of growth conditions, e.g. temperature (Gladish and Rost, 1993). This is the first point: the primary root, of at least the eight species studied, shows a three-part growth cycle followed by reaching a determinate length.

The next point is that the size, shape and behaviour of the RAM does not remain constant during the growth of the root. I will give two examples. In pea, Rost and Baum (1988) measured the RAM at different times during the primary root growth cycle (Fig. 3). They showed that the height of the meristem increased during the accelerative phase of the growth cycle, it remained relative constant in height during the constant phase of the cycle and it became shorter during the deceleration phase of the root growth cycle. The RAM also became narrower and had less volume during the growth cycle. The conclusion here is nicely stated by DeTullio et al. (2010), ‘...RAM organization evolved to become highly plastic and dynamic’. Another example of RAM plasticity is connected to the observation that the primary roots of the examined plants tend to reach a determinate length. In Arabidopsis (Baum et al., 2002) and in five other species (Chapman et al., 2003) with a closed RAM organization, the pattern of the meristem was followed over the growth cycle of the primary root. In each case (Blumenbachia; Fig. 4), the closed pattern of the RAM changed to an open pattern when the primary root reached its determinate length. Furthermore, the cells of the RAM cease cycling and become symplastically isolated (Zhu and Rost, 2000). Incidentally, determinacy in root growth is not restricted to the primary root (Shishkova et al., 2007).

Clearly there are different patterns of cells in the RAM of dicotyledonous plants, and these patterns, which are associated with specific taxa of plants, obviously evolved under different conditions over time. Why are there different conserved patterns, why not just one pattern? There is not any absolute answer to this question, but an observation by Hawes (1991) and a subsequent study by Hamamoto et al. (2005) makes an interesting suggestion.

Hawes (1991) and Hawes et al. (1998, 2003, 2005) made the observation that root caps of many plants release living cells into the rhizosphere in a programmed way. These cells, called border cells, live in the soil environment, may divide and secrete materials into the soil and thereby interact with soil micro-organisms. The numbers of border cells released experimentally was from up to 10 000 border cells in 24 h by a cotton root to no border cells in roots of Brassica (Hawes et al., 2003). It was this observation that led Hamamoto et al. (2005) to ask a broader question connecting RAM organization to root function.

Hamamoto et al. (2005) studied 19 different plant species from different families with all three types of RAM organization. They then examined the anatomy of the root caps, looked for the presence of border cells and tested for living cells using the fluorescein diacetate (FDA) method (O’Brien and McCully, 1981). This examination revealed that roots with an open organization (e.g. Cucumis sativus in Fig. 5; Daucus carota in Fig. 1B) released border cells from the surface of the root cap. FDA staining showed that sunflower and pea border cells showed a positive reaction indicating that the border cells were living when released (Hamamoto et al., 2005). Roots with a closed organization (Salvia; Fig. 6) tended to release their
surface root cap cells in sheets of cells. In *Brassica* these cells did not show a positive FDA test (Hamamoto et al., 2006). In *Arabidopsis* a TUNEL (terminal deoxynucleotidyl transferase dUTP nick end labelling) reaction test showed the surface root cap cells to be undergoing programmed cell death prior to release of the surface root cap cells (Fig. 7) (Zhu and Rost, 2000). The results of these studies show that roots with an open organization release living border cells into the soil environment and roots with a closed organization do not.

**ROOT ORGANIZATION AND THE POSITION OF CONTROL POINTS**

Roots have a deceptively simple body plan (Fig. 8) consisting of cylinders of different tissues, sectors (e.g. xylem and phloem), individual cell files, groups of cells within files and individual cells. All of these levels of structural organization must be considered when trying to sort out how specific events are controlled. Let us briefly look at each level of organization (Rost, 1994; Rost and Bryant, 1996).

Tissues are aggregates of cells with a common origin (meristem) and a common collective function, and in roots they tend to be organized into cylinders of cells and sectors (Fig. 8). Cells within a specific cylinder or sector tend to cycle and differentiate together as a unit. The signals
controlling this obviously affect all cells within the unit and presum-ably move from cell to cell longitudinally, transversely and sometimes tangentially, to the exclusion of tissues of different identity nearby. This shows either that the signal is unique to the cylinder, or that the nearby cells are insensitive to its effect or are structurally (plasmodesmatically) isolated.

Juniper and Barlow (1969), Gunning (1978), Gunning and Overall (1983) and Zhu et al. (1998a, b) examined the distribution of plasmodesmata (PD) in root tips and noted the tissue specificity of the pattern, and that the most abundant frequency of PD was in the transverse cell walls within files of cells. In Arabidopsis (Zhu et al., 1998a) the frequency of PD was lowest in the outer and inner tangential walls, possibly indicating less signalling between cylinders (Fig. 9). The identity of the signal, possibly auxin, is still an open question (Benkova et al., 2009; DeSmet et al., 2010).

The vascular cylinder is organized into xylem and phloem sectors (Rost et al., 1988). Xylem and phloem tissues are composed of a complex of several cell types, vessel members, tracheids, parenchyma cells, pericycle cells, fibres, sclereids, sieve tube members, companion cells, and possibly other cells organized into a pattern unique to each taxa. The differentiation of the cells making up these tissues occurs in a relatively synchronous pattern such that there are multiple xylem sectors separated by phloem sectors the events in the xylem of all sectors occur at the same time. As an example, the pericycle cells in a pea root continue to divide in a transverse plane some distance from the root tip just outside of the three protoxylem points, while cells in the cortex and the pericycle of adjacent phloem sectors are not dividing (Rost et al., 1988). Evidence of this at the molecular level can also be seen in cross-sections of pea roots where, at about 10 mm from the root tip, only pericycle cells in the xylem sector showed a positive signal for labelled histone H2A mRNA (Tanimoto and Rost, 1993; Tanimoto et al., 1993).

Gunning (1982) conducted a series of studies on the organization of the Azolla fern root tip. This fern has a large apical cell that divides acropetally to form root cap initials and sequentially from its three basal surfaces to make a sequence of groups of cells called merophytes. This developmental unit, or merophyte, divides, differentiates and enlarges in a set pattern, resulting in mature cells and tissues. During subsequent development, cell files differentiate in continuity between merophytes, which would necessitate communication between them. A merophyte system has been reported in other lower vascular plants but not in the roots of higher vascular plants. Barlow (1987) described a somewhat analogous structural unit in roots of the cortex of corn, and he called them cell packets. Cell packets are also found in pea roots (Webster, 1980). In Arabidopsis, Wenzel and Rost (2001), and in Trifolium repens Wenzel et al. (2001) reported on how the epidermis and peripheral root cap divide in units that they called a module consisting of a packet of epidermal cells and a packet of peripheral root cap cells. This will be described in detail later.
Cell files are a basic unit of structure in the root where all the cells in a cell file are clonally related to each other and originate in a lineage from a tier or zone of initial cells depending on the RAM organization type. Popham (1955) in a rather classic study examined the location of many different differentiation events in pea roots growing in hydroponic conditions under aerated and non-aerated conditions. The roots grew faster in aerated conditions and more slowly in non-aerated conditions. Popham (1955) sampled roots and measured the position of differentiation events. His noteworthy observation is that the position of differentiation events is tissue specific. Table 1 shows some selected data from his paper simply making the important point that different cell files do different things at different tissue-specific times and locations, and consequently whatever controls these processes needs to also be a tissue-specific process.

Figure 10 illustrates this further, but for cell cycle events, in a general way from pea roots, with diagrams of four different cell files representing xylem pericycle, phloem pericycle, a xylem tracheary element file and a cortical parenchyma file. On the right side of the illustration are the approximate distances from the root body–cap boundary where each event occurs. A note on the pericycle might be useful here. The pericycle is a unique tissue and in the xylem sector it is usually a single cell layer located immediately outside the outermost protoxylem tracheary element. Within the xylem sector the pericycle is the site of the initiation of lateral root primordia. The pericycle cells in the phloem sector are also a single layer, but they have a unique identity and behaviour, as will be discussed later.

Xylem pericycle cells divide in the transverse plane and pass through several rounds of the complete cell cycle. The cells then arrest for a time, then start to cycle again, some lateral root founder cells are then created, and they then continue to cycle and divide, but in a tangential plane. These events would involve cell cycle on/off switches, a cell cycle counter and finally a mechanism to change the orientation of the cell plate at specific lateral root initiation sites.

Phloem pericycle cells are located in the adjoining vascular cylinder sector, but have a much simpler cell cycle control path. These cells divide several times through complete cell cycles, then arrest and never divide again.

Xylem tracheary elements are a water-conducting cell type. They are interesting because they tend to be large cells with a sometimes high ploidy level, they tend to have sculptured secondary cell walls and they go through programmed cell death on the way to reaching their mature function. The procambium primary meristem cells are progenitors of xylem tracheary

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**Table 1. Selected pea root (Pisum sativum) cell differentiation level data from 21-d-old roots grown in liquid medium**

<table>
<thead>
<tr>
<th>Tissue</th>
<th>Distance from root capolumella (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Endodermis cylinder</td>
<td>82</td>
</tr>
<tr>
<td>Pericycle cylinder</td>
<td>82</td>
</tr>
<tr>
<td>Protoxylem</td>
<td>176</td>
</tr>
<tr>
<td>Protophloem</td>
<td>229</td>
</tr>
<tr>
<td>Cortical parenchyma vacuolated</td>
<td>650</td>
</tr>
<tr>
<td>Endodermis casparian bands</td>
<td>3815</td>
</tr>
<tr>
<td>Xylem lignified walls</td>
<td>11 000</td>
</tr>
<tr>
<td>Phloem fibres</td>
<td>26 071</td>
</tr>
</tbody>
</table>

These data make the point that the distance from the root tip where differentiation events occur is tissue specific. Note also that the location of differentiation events is modulated by root growth rate: ‘With few exceptions, levels of tissue differentiation were nearer the apex in non-aerated (slow-growing) than in aerated (faster-growing) roots of comparable age and genotype’ (Popham, 1955, p. 539; data extracted from table 2)
elements and they divide in a transverse plane some number of times through complete cell cycles, then the $G_2 \rightarrow M$ part of their cycle ceases and the cells pass through several rounds of $G_1 \rightarrow S$ to reach some level of ploidy. Coupled with this, the cells lay down their secondary cell wall and initiate programmed cell death.

The last cell file in this illustration is a cortical parenchyma cell type. These cells tend to be fairly large and specialized for storage, often of starch. These cells divide through a few complete cell cycles, then switch to a $G_1 \rightarrow S$ cycle to become polyploidal during the period when they accumulate starch. So, here are four different cell files, all in close proximity, and all having different cell cycle patterns and processes. Since PD are predominantly in the transverse cell walls, this is the most likely pathway for signal transduction, but the identity of the signal, although most likely to be auxin, has yet to be fully understood.

Transition points

In the ‘classical view’ a root tip is considered to be organized into the following regions: the root cap, the meristem, the elongation region and the maturation region (Rost, 1994). These boundaries do not really exist, as we have just discussed, and each cell file, or group of files in a cylinder or sector, tends to act independently. The boundaries between the region of the meristem and the region of elongation, therefore, may be different in cells of the cortex, for example compared with cells of the epidermis or the vascular sectors. The manner in which this happens involves the idea of transition points (Rost, 1994). This concept, originally described by Ivanov (1973), suggests that within each cell file there are developmental switches. One would be the point where cell division is turned off in a phloem pericycle cell file, which would be one file in the procambium primary meristem. Another transition point would exist at the boundary of the elongation region, and another at the termination of cell maturation. In this way each file or group of files may act independently of each other. Exactly what happens at the transition point is not known, but perhaps specific genes are expressed, which turn events on or off in a cell file-specific manner.

The position of transition points, as we have seen, is not static. As the growth rate of a root changes, the location of the transition point also changes (Popham, 1955). An example in cotton is that as the root growth rate speeds up, the position of the maturation of xylem vessel members becomes farther away from the root tip, and as the root growth rate slows down the position of maturation becomes closer to the root tip (Reinhardt and Rost, 1995). This built-in mechanism allows the root to accommodate its growth rate events (cell division and elongation) spatially to its cell differentiation events. In cotton roots a linear relationship exists between root growth rate and the position of protoxylem maturation (Reinhardt and Rost, 1995). Fast growing roots show protoxylem maturation farther from the root tip than do slow growing roots.

Modular development of the epidermis and peripheral root cap

Baum and Rost (1996) reported on the structure of the closed RAM in Arabidopsis thaliana. In that study they reported on the modular structure involved in the development of the epidermis and peripheral root cap which together are clonally related and initiated by a specialized periclinal division of an initial cell they termed the root cap/protoderm (RCP) initial. The idea for a modular structure for the epidermis and peripheral root cap was first put forward by Kuras (1978) in a study of embryo development in Brassica napus, and the basic format and developmental sequence is similar in A. thaliana, which is in the same family, the Brassicaceae. What follows is a description of that sequence as another example of a regulated series of cell cycle behaviour (Wenzel and Rost, 2001).

In median longitudinal view (Figure 11) an Arabidopsis RAM is closed with three tiers of initial cells; the upper tier forms the procambium which differentiates into the vascular cylinder and becomes sectored into primary xylem and primary phloem tissues. The middle tier forms the ground meristem which differentiates into the cortical cylinder with its inner layer the endodermis. The third tier of initials has two components, the columella initials (CIs) which form the layers of the columella root cap, and the RCP initials that form the protoderm/epidermis and the peripheral root cap.

The description of an initial is that it is a ‘meristematic’ cell that divides to renew itself and to form another derivative cell that differentiates into one of many different cell types. The behaviour of these initials and the sequence of divisions progressing from their derivative cells provides an example of very specific cell cycle control. CIs typically consist of four internal cells surrounded by 8–11 outer CI cells (Wenzel and Rost, 2001). The divisions of the CIs is relatively synchronized to produce discrete layers of columella root cap; in the image shown there are four layers (Figure 11). In three dimensions the RCP initials form a circle around the CIs. The RCP initials divide in sequence around the CIs (Baum and Rost, 1996; Wenzel and Rost, 2001). The division of the RCP initial is periclinal, forming a T-division where the ‘shaft’ of the T is the newly formed cell wall. In Figure 11, there are

![FIG. 11. Median longitudinal section view of a Arabidopsis thaliana RAM. The three T-divisions from prior divisions of the root cap/protoderm (RCP) initials are circled. Scale bar = 0.04 mm.](http://aob.oxfordjournals.org/content/images/11)
three T-divisions apparent along one lineage series, shown inside circles on the right side.

Figure 12 illustrates the sequence of divisions that occur to form the root cap and epidermis in *A. thaliana*. The CIs (Fig. 12A) divide in a transverse plane to form the next increment of the columella root cap shown by the letter ‘a’. The adjoining RCP initial will divide in concert with the CI or immediately after it by a periclinal T-division (Fig. 12B). The resulting two cells will divide again, the inner one will renew the RCP initial and form the first increment of protoderm/epidermis and the outer one forms the first two cells of the peripheral root cap. This cluster of a protoderm/epidermal cell and two peripheral root cap cells is the first step in module formation, noting that both components are clonally related and derivatives of the RCP initial. The next step in the process is that the CI will divide again, followed by the next division of the RCP initial so that the columella root cap and the peripheral root cap have components added and grow in concert with each other as shown in Fig. 12B. Figure 12B shows three T-divisions in a lineage sequence and the three modules which form, with number 1 as the oldest.

The division sequence of the modules formed by the T-divisions of the RCP initial follows a fairly consistent pattern. The protoderm/epidermal cell divides four times to form $1 \rightarrow 2 \rightarrow 4 \rightarrow 8 \rightarrow 16$ cells that make up the packet of epidermal cells. This number is quite consistent. After the full increment of 16 cells forms, the cells proceed to elongate. The peripheral root cap cells also progress through a division series $1 \rightarrow 2 \rightarrow 4 \rightarrow 8 \rightarrow 16$ cells to form a root cap packet of cells. The outer layer will eventually pass through programmed cell death (Zhu and Rost, 2000) and be sloughed off as a more or less intact layer. Together, the protoderm/epidermis packet and the peripheral root cap packet make up a module showing a very prescribed and consistent cell division timing sequence and a cell counting mechanism. In a second study, Wenzel et al. (2001) examined the development of the epidermis and peripheral root cap of white clover (*T. repens*) which has an open RAM organization, and it is quite noteworthy that this root also formed modules in the same pattern even though the RAM type was different. The only difference between *Arabidopsis* and *Trifolium* was that the packets tended to be composed of 32 cell of epidermis and 32 cells in the peripheral root cap in the latter, showing that

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**Fig. 12.** Division steps for the development of the columella root cap from the columella initials (CIs), and the epidermis/peripheral root cap modules from the root cap/protoderm (RCP) initials. (A) The inner CI divides prior to the outer CI. (B) Divisions of the outer CI and adjacent RCP initial which generate the three modules are coordinated, 1 is the oldest, 3 is the youngest. (C) Axial divisions in the protoderm, prcA and prcB in the three modules. New divisions are shown with red lines. From Figure 3 of Wenzel and Rost (2001) with permission.
in these roots the module had one more cell division, but it was still a multiple of eight cells.

CONCLUSIONS
1. There are three general RAM types in dicotyledonous angiosperms: basic-open, intermediate-open and closed; the intermediate-open is ancestral.
2. RAM size and shape change with the root growth cycle.
3. The height of a RAM correlates with the root growth rate.
4. Roots with a closed RAM organization have specific initials to which all cells making up the root cap and body are connected by lineage. Roots with an open RAM organization have no specifically identifiable initials cells and consequently the lineage connections for cell files are less clear.
5. Primary roots show a three-part growth pattern and become determinate.
6. The RAM pattern changes when the root reaches its determinate length and the cells of the RAM cease cycling.
7. RAM type is related to root cap function. Roots with a closed apical organization have a smooth outside surface; they tend to slough off their root cap in layers as dead cells and not as individual living border cells. Roots with an open organization release many border cells that continue to divide and secrete substances.
8. Cell cycle and differentiation control points are tissue specific and their position also correlates with root growth rate.
9. The epidermis and peripheral root cap in A. thaliana form through a precise series of cell divisions from a RCP initial cell forming modules of 16 epidermal cells and 16 peripheral root cap cells. A similar pattern occurs in T. repens, a root with an open RAM organization, the difference being that 32 cells form in each packet.

How are these very specific genetic events controlled in a complex tissue?

Rost and Bryant (1996) wrote a review on root organization and gene expression where the authors tried to identify the genes known at that time. Many questions remain unanswered. How many genes are involved in differentiation regulation? Where are these genes activated and how? How do cells ‘communicate’ in cylinders, sectors and files? What is the nature of the communication signals? What is the role of auxin, cytokinin and other regulators? How does positional information regulation work in roots?

It is now left to the current and next generation of scientists to sort out how events are controlled in roots.

ACKNOWLEDGEMENTS
I acknowledge the partnership of many undergraduate and graduate students, post-doctoral scholars and collaborations over almost 40 years of research on root structure and development. I would like to note in particular the work of Jack Van’t Hof, Stuart Baun, Dan Gladish, Gene Tanimoto, Maud Hinchee, Carol Wenzel, Edwin Groot, Sue Nichol, Tong Zhu, Harold Reinhardt, Joseph Dubovsky, Alexander Lux, Arnold Bloom and Jim Seago, and I dedicate this paper to everyone who has passed through my laboratory over the years.

LITERATURE CITED


