J Plant Growth Regul (2003) 21:287–295
DOI: 10.1007/s00344-002-0036-x

J P G R
Journal of Plant Growth Regulation

Primary Root Growth and the Pattern of Root Apical Meristem Organization are Coupled

K. Chapman,[2] E.P. Groot,[1] S.A. Nichol,[2] and T.L. Rost[2]*

[1]*Institute of Systematic Botany, University of Mainz, Bentzelweg 9a, D-55099 Mainz, Germany;* [2]*Section of Plant Biology, Division of Biological Sciences, University of California, Davis, California 95616, USA*

Abstract

Root apical meristems (RAMs) in dicotyledonous plants have two organizational schemes; closed (with highly organized tiers) and open (tiers lacking or disorganized). These schemes are commonly believed to remain unchanged during the growth of the root axis. Individual roots are commonly thought to have indeterminate growth. We challenge these two generalizations through the study of five species with closed apical organization: *Clarkia unguiculata* L., *Oxalis corniculata* L., *Dianthus caryophyllus* L., *Blumenbachia hieronymi* Urb., and *Salvia farinaceae* Benth. cv. ''Strata''. These roots have phased growth patterns where early growth is followed by deceleration, after which the initial cells stop dividing, elongation ceases, and the root reaches its determinate length. At or before reaching determinacy, the root apical meristem stops maintaining its closed organization and becomes less organized. These observations will be placed in context with observations from the literature to suggest two new generalizations, namely, that apical organization does change over the growth phases of roots, and that roots are determinate.

Key words: Root apical meristem; Determinate growth; Dicot primary root

Introduction

The plant body has a bipolar growth axis with a root apical meristem (RAM) at one end and a shoot apical meristem at the other. One traditional idea is that ''the axial organs root and stem... are indeterminate'' (Sinnott 1935). This generalization can be interpreted to mean that the root apical meristem will remain active indefinitely as long as conditions are suitable. Several studies since have shown that the roots of many plants do not grow indefinitely and that they are in fact determinate. Pea (*Pisum sativum* cv. Alaska) (Gladish and Rost 1993), cotton (*Gossypium hirsutum* cv. Acala SJ-2) (Reinhardt and Rost 1995), and *Arabidopsis thaliana* ecotype ''WS'' (Zhu and others 1998) to mention three examples, are species where the primary root is determinate. A typical growth curve for their primary roots had three phases – an initial phase of accelerating elongation soon after emergence, a steady phase of the seedling primary root, and a decelerating phase leading to termination of elongation. The time it takes to reach the determinate length was variable depending on species and environmental factors

Received: 11 September 2002; accepted: 9 December 2002; Online publication: 28 March 2003
Corresponding author; e-mail: tlrost@ucdavis.edu

Table 1. Selected Dicot Species with Closed Root Apical Organization

Family	Species	Determinate Age (d)
Onagraceae	*Clarkia unguiculata* L.	33 days
Oxalidaceae	*Oxalis laxus* L.	14 days
	Oxalis corniculata L.	27 days
Caryophyllaceae	*Dianthus caryophyllus* L.	19 days
Loasaceae	*Blumenbachia hieronymi* Urb.	28 days
Lamiaceae	*Salvia farinaceae* Benth. cv. ''Strata''	41 days

such as temperature. In this paper we will show how determinacy is common in primary roots of five other species in different families, and that there are many other examples in the literature where roots of various types reach a determinate state.

What is the Developmental Basis of Root Determinacy?

Many studies have examined the structure, organization, and cell patterns of the RAM in dicot and monocot plants (summarized in Rost 1994). The simplest and most satisfying organization scheme comes from Guttenberg (1968) who proposes two basic types of RAM – open and closed. The pea root RAM is an example of open, and *Arabidopsis* is an example of closed. The main difference is that closed RAMs have tiers of initial cells at the boundary of the root body and root cap, to which all cell files connect by lineage (Baum and others 2002). Open RAMs lack this precise organization, sharing initial cells between tiers. A third type, called intermediate open, has also been proposed. It has a relatively disorganized center where cell files can be traced to an initial zone, but it has specific initials for the epidermis and root cap (Groot and others 2001b).

Baum and others (2002) reported on the apical organization of the primary root of *A. thaliana*. They showed that in young seedlings the RAM was closed, with three specific initial tiers for the root cap/epidermis, the cortex, and vascular cylinder. As the root grew and aged the organization changed until at four weeks the tier structure was much less organized (intermediate open), especially the central initials associated with the cortex. An interesting correlation to this observation (Zhu and others 1998) was that the frequency of plasmodesmata in cell walls of the root apical meristem (RAM) decreased once it became determinate. This suggested that the primary root stopped elongating and the RAM simultaneously ceased to function when communication among cells diminished. Other published observations support the notion that RAM organization does not remain constant during growth. Rost and Baum (1988) observed that the shape and size of the RAM in peas changed with the age of the primary root. Armstrong and Heimsch (1976) and Seago and Heimsch (1969) found that the RAM organization depended on the age (length) of the root of selected herbaceous species grown from seed. Such observations make it quite clear that the RAM is a dynamic structure, that changes with the growth, developmental age, and environmental conditions of the root. In this paper we will describe five more examples of species where RAM organization changes during root growth, and hopefully we will disband the commonly held generalization that the structure of the root apical meristem (RAM) is static. The present study has two specific objectives: (1) to show that primary roots of the various species become determinate, and (2) to show that primary roots with closed apical organization change to open or intermediate open once the root reaches its determinate length.

Materials and Methods

Five representative species (*Clarkia unguiculata* L., *Oxalis corniculata* L., *Dianthus caryophyllus* L., *Blumenbachia hieronymi* Urb., and *Salvia farinaceae* Benth. cv. ''Strata'') of dicotyledonous plants, all with closed root apical organization (Table 1) were acquired either commercially or from the UC Davis Botanical Conservatory (note that *Oxalis laxus* was used in place of *O. corniculata* for the early time samples). Seeds were surface sterilized for 5 minutes in a solution of commercial bleach with a drop of dish soap followed by a 30-second rinse in 70% ethanol and three rinses in sterile distilled water.

Seeds were germinated in sterile, moist conditions and transplanted before the radicle reached 3 mm in length. Seedlings were grown in either a 25.4 cm length × 60.96 cm height × 6.35 cm width rhizotron made of plexiglass or one of several PVC pipes cut in half lengthwise and covered with clear

acetate. These rhizotrons were lined with germination paper and filled with vermiculite. Seedlings were oriented between the germination paper and plexiglass with the radicle pointing downward so that the roots would grow straight and could be measured from the outside of the rhizotron during the growing period. Seedlings were watered with sterilized 0.5% Hoagland's solution and grown at 25°C for 16 h/day using fluorescent lighting (92–95 $\mu E\ m^{-2}\ s^{-1}$). Wrapping the rhizotrons in aluminum foil minimized effects of light on root growth. Primary root growth was measured by marking the position of the root tip each day on the Plexiglas window. A daily growth rate for each species was calculated. The graphs were based on data collected from the averages of 7 roots for *C. unguiculata,* 12 for *O. corniculata,* 14 for *D. caryophyllus,* 8 for *B. hieronymi,* and 9 for *S. farinacea.*

Root tips were sampled just after emergence and again when the primary root of each seedling stopped elongating, having reached its determinate length. Harvested root tips were fixed overnight in a solution of 1.5% glutaraldehyde, 0.3% paraformaldahyde, and 0.025 M PIPES buffer (piperazine-N, N′-bis [2-ethanesulfonic acid]) buffer (pH 7.2). Specimens were rinsed three times for 15 minutes each in 0.025 M PIPES buffer and passed through a dehydration series from 10% ethanol to 90% ethanol in 10% increments. Specimens were stained in 0.5% Fast Green in 95% ethanol and rinsed with absolute ethanol three times, for 15 minutes each.

Root tips were embedded in Historesin™ Plus (Leica Instruments GmbH, Heidelberg, Germany) or Histocryl™ (Electron Microscope Sciences, Fort Washington, PA) for sectioning. Both resins require the same infiltration process of 3:1, 1:1 and 1:3 ratios (absolute ethanol to resin) for 1 hour each followed by a change of absolute resin for 1 hour and another change overnight in a vacuum. The roots were arranged in aluminum pans and hardener was added to the resin solution to initiate polymerization. The exothermic reaction was controlled in vacuum by placing the aluminum weigh pan on a cooled (−8°C) porcelain plate.

Individual root tips were cut out of the resin with a jeweler's saw and mounted onto 0.47cm diameter wooden dowels with Duco™ cement (Devcon Consumer Products, Riviera Beach, FL). Two-µm thick longitudinal sections were cut on dry, glass knives on a Reichert-Jung model 2050 Supercut microtome (Cambridge Instruments Inc., Buffalo, NY). Sections were placed onto water droplets on gelatin-coated slides and dried on a 60°C slide warmer.

Sections were stained with the periodic acid, Schiff's reagent according to O'Brien and McCully (1981). Briefly, slides were treated with periodic acid for 20 minutes in a 40°C water bath and rinsed in deionized water for 5 minutes. Cell walls were stained with Schiff's reagent for 60 minutes and treated in 0.5% sodium bisulfite three times for 2 minutes each. Slides were then rinsed for 8 minutes in deionized water, and dried on a 46°C slide warmer. For observation, coverslips were mounted temporarily in 70% sucrose. An Olympus Vanox - AHBT photomicroscope and Kodak Elite Chrome160T 35 mm film were used to photograph median longitudinal sections.

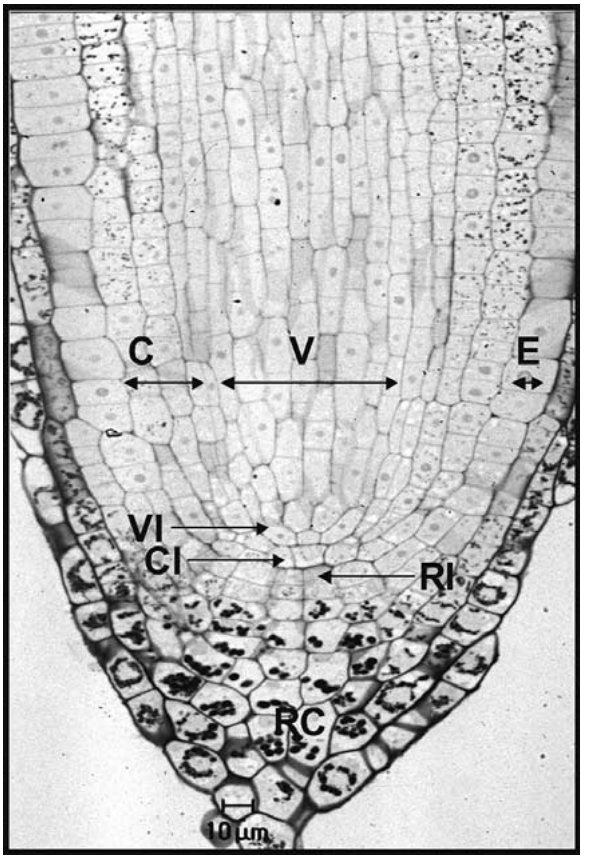

Figure 1. Young *Clarkia unguiculata* primary root with closed root apical organization. The vascular cylinder (V), cortex (C), epidermis (E) and root cap (RC) tissues arise from three distinct tiers of meristematic cells: the vascular initials (VI), cortical initals (CI) and root cap/epidermal initials (RI). Each photograph shows 10 µm line scales.

Results

A typical root with closed apical organization is shown in Figure 1. In this example there are three initial tiers: root cap/epidermis (RI), cortex (CI), and vascular cylinder (VI). These three tiers are directly connected by lineage to the tissues and regions of

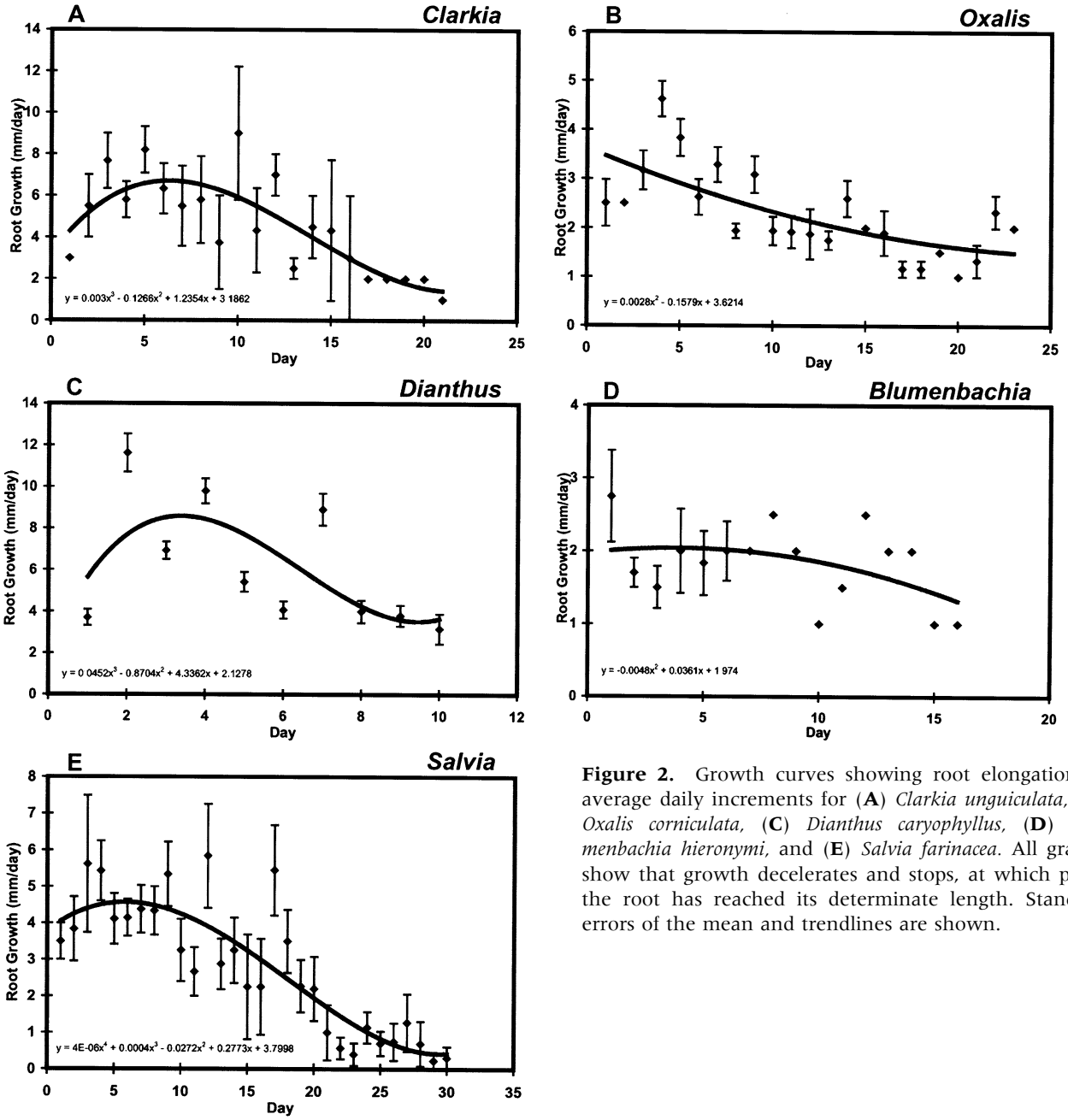

Figure 2. Growth curves showing root elongation in average daily increments for (**A**) *Clarkia unguiculata,* (**B**) *Oxalis corniculata,* (**C**) *Dianthus caryophyllus,* (**D**) *Blumenbachia hieronymi,* and (**E**) *Salvia farinacea.* All graphs show that growth decelerates and stops, at which point the root has reached its determinate length. Standard errors of the mean and trendlines are shown.

the root as labeled – root cap and epidermis, cortex and vascular cylinder.

The primary roots of all five tested species eventually reached a determinate length. The growth rate and time to reach determinacy was different for each. The maximum daily growth rates for *B. hieronymi* and *O. corniculata* was near 2 mm per day, *C. unguiculata* and *S. farinaceae* 5.5 mm per day, and *D. caryophyllus* about 8 mm per day (Figure 2). The graphs in Figure 2 show trends in the average daily growth of each of the five species. The graphs usually suggest an initial accelerating phase, a period of steady growth, followed by a decline and a final termination of growth. The age at which each species reached this determinate point varied between 3 and 5 weeks (Table 1).

Each species showed change in root apical organization from early seedling development to maturity at its determinate root length. *C. unguiculata* as a young, 2-week-old seedling had closed organization with distinct tiers of initials (Figure 3A). The young *C. unguiculata* epidermal/root cap initials could be traced apically to the columella, and basally to the peripheral root cap and epidermis through

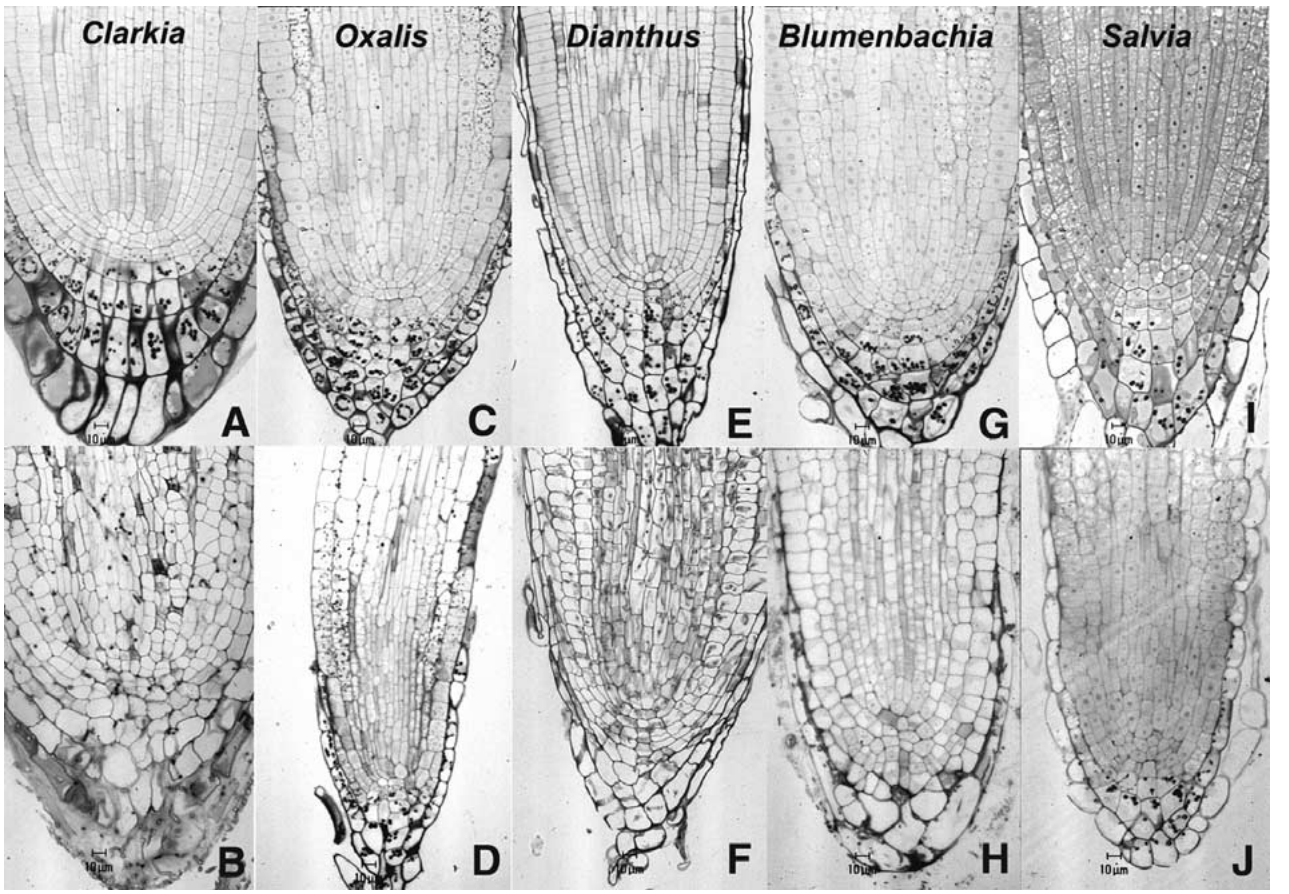

Figure 3. Comparison of five dicotyledonous species showing changes in root apical organization over time. Mature roots have changed from their younger closed form (see Fig. 1 for initial tier and tissue labels) to become disorganized and usually change to intermediate open. (**A**) young *Clarkia unguiculata,* (**B**) mature *Clarkia unguiculata,* (**C**) young *Oxalis laxus,* (**D**) mature *Oxalis corniculata,* (**E**) young *Dianthus caryophyllus,* (**F**) mature *Dianthus caryophyllus,* (**G**) young *Blumenbachia hieronymi,* (**H**) mature *Blumenbachia hieronymi,* (**I**) young *Salvia farinacea,* and (**J**) mature *Salviafarinacea.*

anticlinal cell divisions. The cortex initial tier had two irregular layers. Vascular cylinder initials are also distinct from other tissues. By 33 days the organization pattern was considerably less distinct in two of seven roots sectioned (Figure 3B). Cell files from all tissue layers basipetal to the meristem lost some regularity in cell shape and size. The epidermal/root cap files could be traced by lineage only to a certain region, at which point a wide and indistinct zone of initials was present rather than single tier (Figure 3B). The cells in this zone trace to multiple tissue types and could be easily identified as the progenitor of any cell file or specific tissue. The cells in the apical-most root cap tier collapsed. The organization type in the determinate state of *C. unguiculata* could be classified as intermediate open.

The primary root apical meristem of *Oxalis* (Figure 3C) changed over time in much the same way as *C. unguiculata.* At two weeks, *O. laxus's* root apical meristem had closed apical organization. The epidermis and root cap regions traced directly to the epidermal/root cap initial tier. The single layer of cortical initials led exclusively to the cortex, and the vascular initials to the vascular cylinder. After 27 days, 8 of 12 roots of *O. corniculata* showed the meristem becoming less organized. The cell files lost some of their uniformity in cell shape and size. The epidermis did seem to trace to a single tier of initials, however, several columella files traced vertically to the cortex initial tier, indicating that the RI and CI were shared initials (Figure 3D). The cortical initials were irregularly shaped, but the vascular tissues appeared undisrupted. Another morphological change was that the overall size of the root tips decreased in *O. corniculata* as the root aged, perhaps because the meristem activity slowed to a stop.

D. caryophyllus had closed organization at one and a half weeks (Figure 3E). Three distinct tiers of initials connected to distinct tissue types. At 19 days, 8 of 14 roots confirmed that this organization had

changed, not so much in organization as in a dramatic alteration in the size and shape of the meristem cells (Figure 3F). Although cell files were still fairly aligned and uniform, cells near the meristem and in the root cap were more irregularly shaped than in the younger roots. The epidermal cell file followed through the epidermal/root cap tier of initials, but vertical columella cell files continued upward into the region of cortical initials. The cortical initials and cell files surrounding them were not yet as disorganized as those seen with the mature *O. corniculata.* The vascular initials were completely undisturbed. Mitotic figures were never seen in these late stages; the cells were highly vacuolated and plasmolyzed suggesting that the meristem were not functioning in *D. caryophyllus* at this time.

B. hieronymi was another clear example of closed organization (Figure 3G) with initial tiers tracing distinctly to their tissue types. At 28 days, the clear organization was lacking and the identity of the cells in this zone was unclear. In the determinate root the cortical tiers were disrupted. The columella cell files seemed to connect to the cortical tier (Figure 3H). Four roots of eight were confirmed to show these changes. Cells of the RAM in determinate roots appeared more vacuolate than in those of the young root. The one-week-old root was larger in girth and meristem size than the determinate root.

Like *C. unguiculata, S. farinacea,* as a young root with closed organization also had two layers of cortical initials. The young closed meristem of *S. farinacea* had cell files uniform in cell shape and size, which led distinctly to their respective tissues (Figure 3I). Upon reaching its determinate length at 41 days, the overall sizes of the root tip, meristem, and root cap decreased (Figure 3J). With respect to the root cap, younger roots were six cell layers thick at the widest point from the epidermal/root cap initials to the periphery of the root cap, whereas mature roots were only 3-4 cell layers wide. The meristem in the determinate root lost its ordered initials and appeared more like intermediate open. The CI and RI were shared. Six roots of the nine from this species confirmed these changes in organization and meristem size.

Discussion

Roots of flowering plants terminate in a root apical meristem (RAM). The RAM is organized in one of two basic patterns – open or closed (Guttenberg 1968). We know from phylogenetic studies that open organization, or more precisely intermediate open, is an ancestral condition and closed is derived (Groot and others 2001b). We know also that apical organization is not constant and that meristem size and cell division behavior is a function of root growth and, in seedling roots, the developmental age of the primary root (Baum and Rost 1988; Gladish and Rost 1993; Rost 1994). An old, perhaps anecdotal idea is that root apical meristems are indeterminate; that is, if conditions are right the RAM can function indefinitely. More recent evidence indicates that this might not be the case in many and perhaps all roots. In this study we have reported several observations that support this point, and we will now place those observations in the context of other root growth examples.

In the current study we report that the primary root of five different species (*Clarkia unguiculata* L., *Oxalis corniculata* L., *Dianthus caryophyllus* L., *Blumenbachia hieronymi* Urb., and *Salvia farinaceae* Benth. cv. ''Strata'') from different families become determinate. In these cases the fundamental growth pattern consisted usually of an early accelerated phase followed by a steady rate and then by deceleration and finally termination of growth. In the deceleration phase RAM organization changes to intermediate open, cell shape becomes irregular and vacuolation increases.

These studies are not the first to show determinate root growth and several other examples have been reported. One instance is cluster roots or ''proteoid roots'' that occur in all species of the family Proteaceae and in species from seven other families. These plants tend to grow in nutrient poor conditions (Denkelaker and others 1995; Lamont 1972a, 1972b; Skene 1998). The characteristics of cluster roots are that closely spaced lateral roots are initiated along a root axis, they stop elongating and reach a short determinate length. Cell differentiation occurs all the way to the root tips, and their RAMs stop functioning (Skene and others 1998). These roots become determinate at much shorter lengths (mm rather than cm) than seedling primary roots. One interesting finding is that cluster-type determinate roots can be induced experimentally by root tip excision and treatment with auxin coupled with auxin-transport inhibitors, for example, *Pisum sativum* (Hinchee and Rost 1992).

Another example of this kind of determinate growth behavior is in the development of adhesive pads in the climbing fig, *Ficus pumila* (Groot and others 2003). In this vine, small clusters of 30 to 50 adventitious roots are initiated toward a surface substrate just basal to a node. These roots elongate to between 2 and 5 mm in length, then cease elongation. Root hairs are induced all the way to the

root tip and finally their RAM stops functioning. These roots then secrete a sticky substance effectively sealing the roots to each other, forming an adhesive pad, which then adhere the vine to a substrate. These roots are adventitious, but their developmental behavior is almost exactly the same as those in cluster roots: both are determinate, both show cellular differentiation right to their tips, and both terminate their meristem activity.

Another well-documented example of determinate roots is in members of the Cactaceae (Dubrovsky 1997; Dubrovsky and Gómez-Lomeli personal communication). In *Stenocereus thurberi* and other cactus species, Dubrovsky (1997) has documented that no primary root is indeterminate. All roots elongate for a few days and then slow down and finally cease elongation as soon as three days after emergence. Observations of the root apical meristem revealed no cycling cells and that cell differentiation occurred right to the root tip. He suggests that the purpose of the dysfunction of the RAM was to allow for the stimulation of lateral roots. Dubrovsky adds that cactus lateral roots also reach determinacy, which is related to the temporary availability of water in arid environments. Dubrovsky and Gómez-Lomeli (personal communication) showed further that determinate root growth could be experimentally induced by water stress in another cactus, *Pachycereus pringlei.*

Corn (*Zea mays*) produces determinate lateral roots (Varney and McCully 1991) which tend to be short and lose their RAM function. Over time these roots experience cortical death and finally become nonfunctional (Wang and others 1994). *Euphorbia esula,* the leafy spurge, offers another example of determinate root growth (Raju and others 1963). This noxious weed produces both long and short roots. Short roots elongate to less than 2 cm and then stop growing; these are determinate. Long roots seem to continue elongating, but in some instances their meristem stops functioning, and a lateral root near the tip elongates in the same direction, creating a sympodial set of branches. In those cases the long roots are also determinate.

Roots of *A. thaliana* have closed root apical organization with three distinct initial tiers (Baum and others 2002). The primary root elongates by first rapid growth and then gradually stops when it reaches its determinate length (Zhu and others 1998). Anatomical analysis of root tips during this growth period showed that the structure of the initial tiers change with root age. The central initial tier changed from one layer to two and then by four weeks became disorganized (Baum and others 2002). At its determinate length the RAM looks like it has changed to intermediate open organization, with cell files in the columella seemly extending through the previous site of the no longer present root cap/protoderm initial tier. The cells of the RAM also appear vacuolate and apparently no longer function as a meristem.

Heimsch and his students at Miami University (Oxford, Ohio) published a series of papers starting in the late 1960s on how the apical organization pattern in the roots of members of the Convolvulaceae, Asteraceae, Malvaceae, and Solanaceae change with the growth of the root. We will mention just two of those studies. Seago and Heimsch (1969) studied the primary root tips of many species of the Convolvulaceae and reported the anatomy of the RAM over time, from the embryo through germination and seedling growth. In most instances the RAM started with closed organization and ended with open. Armstrong and Heimsch (1976) studied RAM structure in several species of Compositae (Asteraceae) during stages of root elongation. The RAM in all cases had closed organization in the radicle prior to germination. During elongation some roots stayed in the closed condition throughout the experiment, and others changed to open. Our experience with *Echinacea purpurea* was that the primary root grew past the bottom of the container before becoming determinate. It might be the case for the examples reported by Armstrong and Heimsch (1976) that roots of some species reached their determinate length and transitioned to open and others never reached a final determinate length during the duration of the experiment and therefore stayed closed. The Heimsch papers, in addition to Baum and others (2002), and our studies all show changes in the primary root meristem.

The small floating fern, *Azolla,* has a simple vegetative body with small roots that emerge under the frond. These roots elongate to a few centimeters and then stop. Gunning (1982), in a series of classic papers, did a careful analysis of the root apical meristem of these small determinate roots. He discovered that the apical cell of these roots divide only a set number of times and then stop. The wedge-shaped cells that are derived from the apical cell then also divide a set number of times; these are merophytes, producing the cells that make up the body of the root. These root apical meristems have a built-in counter that regulates the number of times the apical cell and all other cells are able to divide, which is the basis of its root determinacy.

The idea of cell division counters in the meristem has been explored and expanded to flowering plants. Dubrovsky (1997) noted that cells of

the primary root meristem in several cactus species had a consistent number of divisions before growth exhaustion. For one species, *Stenocereus gummosus,* just 3–4 cell division cycles preceded determinacy. This kind of timing is very likely under genetic control. Cheng and others (1995) isolated two mutants, *rml1* and *rml2,* in *Arabidopsis* roots. Embryos of these mutants started to germinate but due to limited cell division they terminated growth. These authors interpreted this observation to mean that the RML gene activates the cell cycle in the root apical meristem. Without this gene being expressed the root apical meristem could not function.

Kaya and others (2001) recently published their findings on a group of genes named FASCIATA that appear to maintain the function and organization of the initial cells in the meristem. This gene group has been associated with shoot apical meristem maintenance, but Kaya and others have further correlated it to RAM organization. The FAS genes are not required for the formation of the RAM, but have a critical function in growing roots. *A. thaliana* mutants not expressing the FAS genes lacked meristem organization and normal division by the initial cells. Descriptions of the developed roots were very similar to those found in the determinate roots in this study.

Root determinate growth may be explained by genetic regulation of cell cycle events. The primary root and lateral root RAM is perhaps viable for only a certain time, because its cells might be capable of cycling only a set number of times. Once initial cells fall out of activity, the meristem is left to appear disorganized. Once new cells are no longer provided to the root body, the axis would stop elongating, and cell differentiation would continue toward the tip. This seems to be the case in the broad set of examples we have outlined.

Evidence is discussed to suggest that roots are determinate structures that eventually cease to elongate when their RAM ceases to function. Except for the case of specialized structures such as cluster roots and adhesive pads, stimulation of branch root production ensures continued development of the root system after a determinate event. The length and age at which a root ceases growth depends apparently on the numbers of cell cycles, environmental conditions and special adaptations. Mutations indicate that RAM function is under genetic control, and that meristem initiation is separable from its maintenance. The minimum lengths of determinate roots are a few millimeters, but the maximum lengths are unknown experimentally due to constraints on the apparatus used to follow root growth. When a root reaches its determinate length its RAM loses its organization. Roots with closed RAM organization become open and cell shape becomes irregular. Plasmodesmata frequency decreases, indicating the cessation of intercellular communication, and finally the cells of the RAM become vacuolate and lose their meristematic identity and potential.

ACKNOWLEDGMENTS

Shelly Duplessis, Lesley Hamamoto and Eileen Sweeney are acknowledged for their assistance in this study. Dr. Wendy Silk is also acknowledged for the loan of her rhizotron.

REFERENCES

Armstrong JE, Heimsch C. 1976. Ontogenetic reorganization of the root meristem in the Compositae. Am J Bot 63:212–219.

Baum SF, Dubrovsky JG, Rost TL. 2002. Apical organization and maturation of the cortex and vascular cylinder in *Arabidopsis thaliana* (Brassicaceae) roots. Am J Bot 89:908–920.

Cheng J, Seeley KA, Sung ZE. 1995. RML1 and RML2, *Arabidopsis* genes required for cell proliferation at the root tip. Plant Physiol 107:365–376.

Denkelaker B, Hengeler C, Marschner H. 1995. Distribution and function of proteoid roots and other root clusters. Bot Acta 108:183–200.

Dubrovsky JG. 1997. Determinate primary-root growth in seedlings of Sonoran desert Cactaceae; its organization, cellular basis, and ecological significance. Planta 203:85–92.

Gladish DK, Rost TL. 1993. The effects of temperature on primary root growth dynamics and lateral root distribution in garden pea (*Pisum sativum* L., cv. ''Alaska''). Env Exp Bot 33:243–258.

Groot EP, Chapman K, Rost TL. 2001a Root apical meristem organization is a dynamic character in dicot roots (Abstracts). Annual meeting of the Botanical Society of America, Albuquerque, NM. p 21.

Groot EP, Nichol SA, Doyle JA, Rost TL. 2001b. Phylogenetic relationships and root apical meristem organization in the dicots (Abstracts). Annual meeting of the Botanical Society of America, Albuquerque, NM p 21.

Groot EP, Sweeney EJ, Rost TL. 2003. Development of the adhesive pad on climbing fig (*Ficus pumila*) stems from clusters of adventitious roots. Plant and Soil. 248:85–96.

von Guttenberg H. 1968. Der primäre Bau der Angiospermenwurzel.Handbuch der Pflanzenanatomie. Band VIII, Teil 5. Berlin: Gebruder Borntrager.

Gunning BES. 1978. Age-related and origin-related control of the numbers of plasmodesmata in cell walls of developing *Azolla* roots. Planta 143:181–190.

Hinchee MAW, Rost TL. 1992. The control of lateral root development in cultured pea seedlings. II. Root fasciation induced by auxin inhibitors. Botanica Acta 105:121–126.

Kaya H, Shibahara K, Taoka K, Iwabucchi M, Stillman B, Araki T. 2001. FASCIATA genes for chromatin assembly factor-1 in *Arabidopsis* maintain the cellular organization of apical meristems. Cell 104:131–142.

Lamont B. 1972a. The morphology and anatomy of proteoid roots in the genus *Hakea.* Aust J Bot 20:155–172.

Lamont B. 1972b. 'Proteoid' roots in the legume *Viminaria juncea.* Search 3:90–91.

Raju MVS, Steves TA, Coupland RT. 1963. Developmental studies on *Euphorbia esula* L. morphology of the root system. Can J Bot 41:579–589.

Reinhardt DH, Rost TL. 1995. On the correlation of primary root growth and tracheary element size and distance from the tip in cotton seedlings grown under salinity. Env Exp Bot 35:575–588.

Rost TL. 1994. Root tip organization and the spatial relationships of differentiation events. In: Iqbal M, editor. Growth Patterns in Vascular Plants 1994. Portland, Oregon: Dioscorides Press, p 59–76.

Rost TL, Baum S. 1988. On the correlation of primary root length, meristem size and protoxylem tracheary element position in pea seedlings. Am J Bot 75:414–424.

Seago JL, Heimsch C. 1969. Apical organization in roots of the Convolvulaceae. Am J Bot 56:131–138.

Sinnott EW. 1935. Botany Principles and Problems. New York: McGraw-Hill Book Company, Inc. p 525.

Skene KR. 1998. Cluster roots: some ecological considerations. J Ecol 86:1060–1064.

Varney GT, McCully ME. 1991. The branch roots of *Zea*. II. Developmental loss of the apical meristem in field-grown roots. New Phytol 118:535–546.

Wang XL, McCully ME, Canny MJ. 1994. The branch roots of *Zea*. IV. The maturation and openness of xylem conduits in first-order branches of soil-grown roots. New Phytol 126:21–29.

Zhu T, O'Quinn RL, Lucas WJ, Rost TL. 1998. Directional cell-to-cell communication in the *Arabidopsis* root apical meristem. II. Dynamics of plasmodesmatal formation. Protoplasma 204:84–93.