

# What the Distribution of Cell Lengths in the Root Meristem Does and Does Not Reveal About Cell Division

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## ABSTRACT

Roots have long been realized to be useful material for studies of cell division. Despite this long history of use, the behavior of cells in the meristem is often misinterpreted. A common error is to argue that differences in cell length reflect differences in cell division rate. In this article we explain the fallacy behind this argument and show how the analysis of cell length distribution can lead to insight about the root meristem. These observations support a model for the root meristem where cells of various tissues grow at the same relative growth rate and divide at the same frequency, indicating that these growth parameters are built into the cells at a fundamental

level. The differences in cell length between various tissues appear to arise at their formation, first at the tissue initials and ultimately in the seed. Length differences among mature cells may be enhanced by differences in the location within the meristem where division ceases. Discovering mechanisms regulating the length of initial cells and the position where cells cease division requires a realistic understanding of how growth constrains the division behavior of dividing cells.

**Key words:** Cell cycle; Cell length; Elongation; Proliferative fraction; Root meristem

## GROWTH OF PLANT CELLS WITHIN AN ORGAN

In a growing animal organ, cells move and change places with their neighbors, whereas in a growing plant organ, cells share cell walls and are thus not able to move independently. We will refer to this style of growth, with cells united to their neighbors "symplastic." However, we do not suggest that this type of growth is caused by the symplast as opposed to the apoplast. Because of symplastic growth, the

pattern of cell dimensions contains information about cell proliferation within that organ (Ivanov 1974), information that is useful and even quantitative, but not always extracted correctly. Here, we describe how the pattern of cell length relates to cell proliferation in the root meristem, because the essentially one-dimensional growth and strict spatial zonation make this organ an ideal case study. However, the concepts described can be generalized to any organ.

For the root, an important consequence of symplastic growth is that, at a given distance from the tip, all cells have the same relative elongation rate. Otherwise, cells with different relative elongation rates and sharing a longitudinal cell wall would distort the root. When differences in growth rate are

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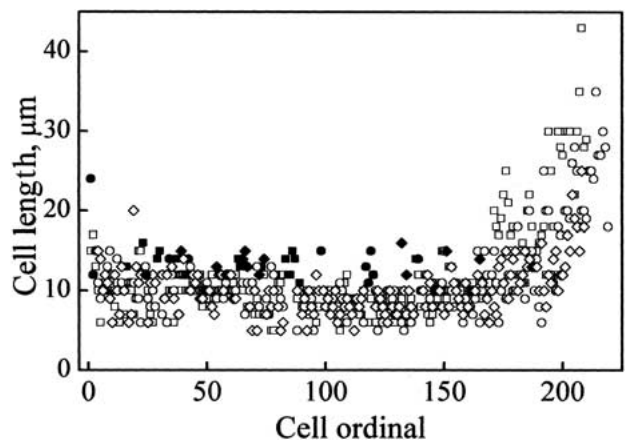
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organized coherently from high on one side of the root to low on the other, then the root will bend, as, for example, when a root responds to gravity. A growth difference between longitudinal neighbors can be induced by certain treatments that inhibit the elongation of epidermal cells more than other tissues: When this occurs, the epidermal cells rupture because of the continued elongation of the underlying cells (for example, Brumfield 1953; Yamamoto and others 2001). Note that in contrast to elongation, expansion rates in orthogonal directions (that is, radial and tangential expansion) can and do differ between tissues at the same position from the tip (Liang and others 1997). Because of this constraint imposed on elongation by the symplastic condition, namely, that at a given distance from the tip, the relative elongation rate does not vary between tissues, any observed difference in cell lengths between tissues must reflect differences between them in cell proliferation (Ivanov 1974; Green 1976).

### ARE ALL CELLS WITHIN THE MERISTEM PROLIFERATING?

A persistent controversy about the root meristem is whether all cells divide. Some authors have argued that cells exit the cell cycle anywhere within the meristem and have introduced the term “proliferative fraction” to account for this variable proportion of dividing cells (Clowes 1976). Values reported for this fraction have ranged from 1 (100% proliferative cells) to around 0.5 (50% proliferative cells). Values less than 1 are obtained in experiments with labeled DNA precursors, such as tritiated thymidine (for example, Evans and Van't Hof 1975). While such labeling methods suffer from a variety of conceptual and technical pitfalls (Green 1976; Webster and MacLeod 1980; Ivanov 1981; Baskin 2000), the constraint of symplastic growth offers a simple way to see if dividing cells exit the cell cycle while still within the meristem.

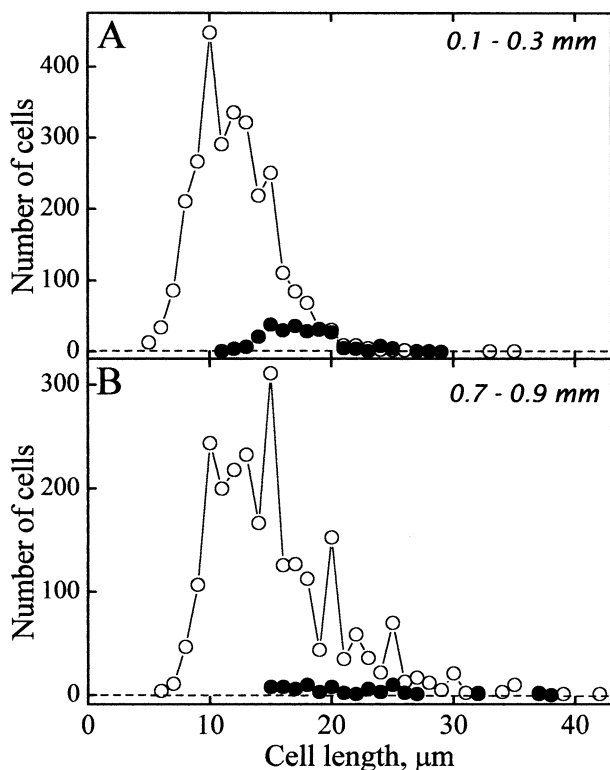
Because of symplastic growth, a cell that misses a mitosis will become larger than its neighbors. It is true that single cells, such as protozoa or cells in culture, often stop expanding when they enter M-phase (Mitchison 1971); however, in a symplastically growing root tip, expansion of a mitotic cell must continue uninterrupted, driven by growth of the neighbors. Therefore, one may determine how many mitoses a cell has missed from the distribution of cell length. For cells of a given tissue and location, the length of a cell depends on its elongation history, length at cytokinesis, and the time since



**Figure 1.** Cell length versus the order of the cell in a file. Data are for cortical cells of maize from three different files (squares, circles, diamonds each represent cells of a single file). At a cell number between 160 and 180, interphase cell lengths ( $\circ$ ,  $\square$ ,  $\diamond$ ) become large while mitotic cells ( $\bullet$ ,  $\blacksquare$ ,  $\blacklozenge$ ) are absent, suggesting that this rank marks the terminus of proliferative activity. In the regions where mitoses occur, interphase cells are rarely longer than mitotic cells. This supports the idea that all meristem cells proliferate (that is, the proliferative fraction equals unity) because cells that miss a cycle must become longer than their neighbors.

cytokinesis. The elongation history will be essentially the same for all cells at a given location because of symplastic growth. As the time since cytokinesis becomes longer than one cell cycle, the length of the cell will exceed the average length of mitotic cells. Therefore, the analysis of the diversity of cell length at a given location reveals how many cells have an apparent cell cycle duration that exceeds the normal range and so may be considered no longer proliferative.

When the length of mitotic and interphase cells is compared in individual files, almost all mitotic cells are larger than interphase cells (Figure 1; Ivanov 1971; Demchenko 1975). In the study represented by Figure 1, the interphase cells that are longer than nearby mitotic cells amount to about 1% of the population, and these cells exceed the length of the mitotic cells only slightly. The same conclusion is reached from plots of the distribution of mitotic and interphase cell length for a given tissue and location (Figure 2). From these data we can conclude that in the meristem the proliferative pool is essentially 100% and all cells remain in the cell cycle. A similar conclusion was reached for the *Arabidopsis* root cortex by finding that the distribution of relative cell length in the apical part of the meristem did not differ significantly from that of the mature zone (Beemster and Baskin 1998). Conversely, we know of no data



**Figure 2.** Frequency distribution of the lengths of interphase, (○) and mitotic (●) cortical cells at two different positions of the wheat root meristem. (A) 0.1–0.3 mm from the tip; (B) 0.7–0.9 mm from the tip. Interphase cells are shorter or equal to mitotic cells with rare exception. Unpublished data are from N.P. Demchenko.

that show cells of a tissue in interphase consistently exceeding the length of nearby mitotic cells, as required by a proliferative fraction less than 1.

In the basal part of the meristem, the length of the longest mitotic cells is invariably exceeded by a few interphase cells (Figure 2B). This arises because cells in different files of the root may cease division at different locations. That certain tissues cease division ahead of others is obvious for those tissues for which the difference is extreme. For example, vascular cells, particularly metaxylem, cease division closer to the tip than other tissues, whereas pericycle cells may continue to divide throughout the elongation zone (Rost and others 1988; Dubrovsky and others 2000). Nevertheless, small differences in the position where division ends may occur even among different files within a single tissue.

Differences among tissues in the position where division ceases may explain some reports of apparently large differences in cell length, differences that were used to infer different cell cycle durations (Bertaud and others 1986; Evans 2000). For exam-

ple, Clowes (1976) reported that, at 1.2 mm from the maize root tip, cell length in various files of the stele differed by as much as a factor of 11. However, xylem and phloem cells cease division far closer to the tip than do parenchyma and in the above-mentioned studies the files with divergent cell lengths were not identified as to cell type. A heterogeneity of cell length in the basal region of the meristem does not necessarily indicate different cell cycle duration.

Thus, the analysis of the diversity of cell lengths permits us to conclude that cells remain in the cell cycle continuously until reaching the position where they exit. Apical of this position, all cells are proliferative. The position where cells exit the cell cycle is the basal terminus of proliferation within a file, and this position differs between tissues and perhaps even among files in a single tissue. Failure to account for the different locations where division stops will lead to the spurious inference of cell cycle heterogeneity.

## DIVERSITY OF CELL LENGTH AND THE VARIATION OF CELL CYCLE DURATION

Another persistent controversy about the root meristem concerns cell cycle duration: It is often assumed that cell cycle duration varies widely between different locations or tissues. Certainly, cells in the developmental organizing center of the root, the quiescent center, have longer cell cycle times than other cells in the meristem (Clowes 1961). The quiescent center cells are highly specialized and their low rate of cell division may be one feature of their differentiation. Cells of the quiescent center are not included in the following discussion.

Cell division rates have been measured kinematically as a function of position for several species and in different laboratories. In some reports, cell division rate is essentially constant with position (Hejnowicz 1959; Beemster and Baskin 1998; Muller and others 1998); whereas in others, division rate varies across the meristem in a bell-shaped curve (Erickson and Sax 1956; Goodwin and Avers 1956; Hejnowicz 1956; Sacks and others 1997). The reason for this discrepancy is not clear. Kinematic methods are prone to errors from curve-fitting, and it has been noted that the papers reporting bell-shaped curves have few data points within the meristem (Hejnowicz 1959; Baskin 2000). Alternatively, it may be that the profile of cell division rate is constant under some conditions and bell-shaped under others.

If the bell-shaped pattern were true, then the approximate constancy of cell length across the

meristem means that the profile of relative elongation rate must also be bell-shaped. This follows because cell length reflects the balance between elongation and division; consequently, to maintain constant cell length, any change in division rate must be balanced by an equal change in elongation rate (Green 1976). To our knowledge, the profile of relative elongation rate has never been reported to vary as a bell-shaped curve within the meristem. Therefore, the assumption of a bell-shaped profile for cell division rate in the root meristem is not supported.

Even without kinematic data, the pattern of cell length in the meristem contains useful information about proliferation activity. Between tissues, cell length differs, typically by a factor of 4 and sometimes more (Balodis and Ivanov 1970; Demchenko 1975; Webster 1980; Ivanov 1981; Evans 2000; Dobrochaev and Ivanov 2001). Differences in cell length are widely assumed to reflect differences in cell cycle duration; however, this assumption is not necessarily correct.

The inability of cell length alone to report cell cycle duration can be seen by considering a quantitative relation between the relevant quantities. For an exponentially growing cell, in a time interval  $\tau$  equal to one cell cycle, a cell grows from its length at birth,  $L_0$ , to its length at mitosis,  $L_m$ , according to the following equation:

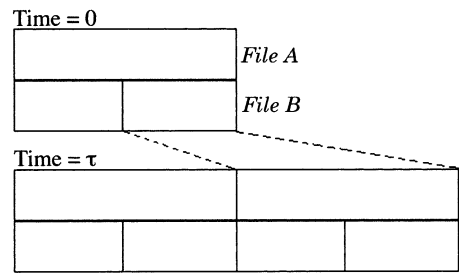
$$L_m = L_0 e^{\tau k} \quad (1)$$

where  $k$  is relative elongation rate. Solving this equation for the cell cycle duration gives:

$$\tau = \frac{1}{k} \ln \left( \frac{L_m}{L_0} \right) \quad (2)$$

Thus, the duration of the cell cycle is not a function of cell length *per se* but instead depends on the ratio of the length of a cell after mitosis to that at the following mitosis. Consequently, the observation of different cell lengths, mitotic or average, does not in itself indicate differences in cell cycle duration; a difference in cell division rate is indicated only if the ratio of mitotic to postmitotic cell length is different (and provided that differences in relative elongation rate, if any, are accounted for). To see this another way, long cells growing beside short cells, because of symplastic growth, both double during the same time interval (Figure 3).

It can be seen from Equation (2) that changes in the ratio of mitotic to just-born cell length provides a relative measure of the cell cycle duration. While the absolute value of the cell cycle duration cannot be known without an independent measurement of

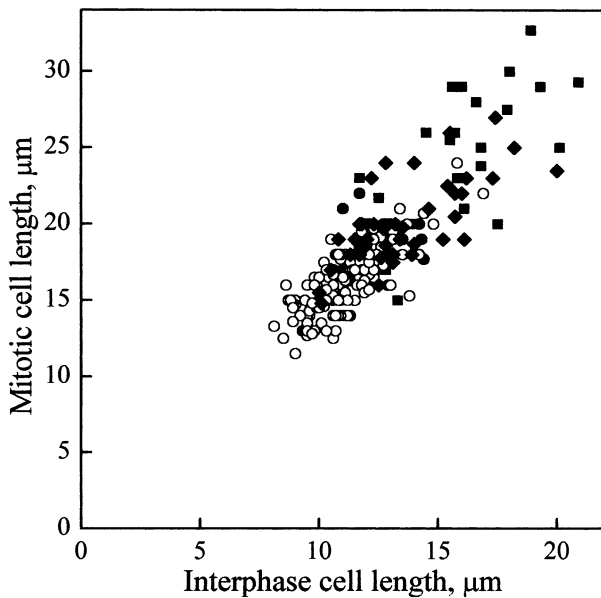


**Figure 3.** Two cell files have the same rates of relative elongation and cell division such that cell length and cell number each double in time =  $\tau$ . Under these conditions, the cell length difference between the files is preserved.

the relative rate of elongation, because that rate must be the same for all tissues (even though it may change with position), differences in cell cycle time can be inferred validly for different tissues or cell files, provided that cell lengths have been measured appropriately.

The variation in the length of mitotic cells was analyzed in detail for both maize and wheat by Dobrochaev and Ivanov (2001). Interestingly, a considerable amount of variation in length among cells was explained by a correlation between the lengths of mitotic and interphase cells within individual files (Figure 4). Note that the data points in this figure specifically truncate the files to exclude apical cells near the quiescent center and cells near the terminus of the meristem which may have ceased proliferation. The correlation shows, apparently for the first time, that a given proliferating tissue in the root meristem contains files with distinct distributions of cell length (that is, files with long cells and files with short cells). These data suggest that, for all files, the ratio of the length of mitotic cells to length of postmitotic cells was constant, indicating a constant cell cycle duration [Equation(2)], although different cell cycle durations cannot be ruled out. This explanation accounts for the differences in cell size among files as arising from differences in the length of initial cells, propagated along the file by virtue of symplastic and exponential growth. Likewise, differences in initial cell length rather than in cell division rate appear to account for the different average lengths of trichoblasts and atrichoblasts in the epidermis of Arabidopsis (Beemster and Baskin 1998). It would be interesting to use living roots to determine whether identified “large-celled” and “small-celled” files retain their distinct status over time.

Another way in which cell length patterns can provide meaningful information is by analyzing the lengths of sister mitotic cells. The ratio of cell lengths



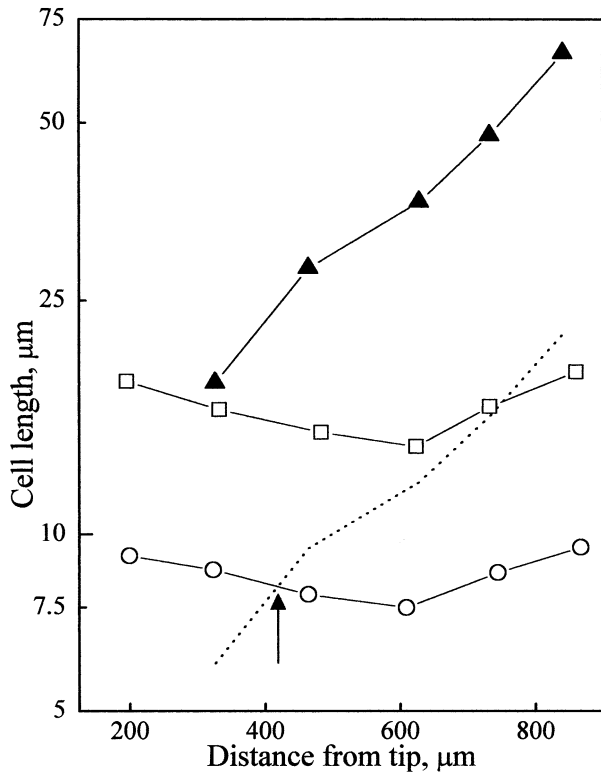
**Figure 4.** Average length of mitotic cells versus average length of interphase cells. Each symbol represents a different file of epidermis (■), exodermis (●), cortex (○), or endodermis (◆). Cells between 200 and 450  $\mu\text{m}$  from the tip were used, thus excluding cells from the quiescent center or from the base of the meristem where cell length might depend on position. Despite the variation in average cell length between different files of the same tissue, average lengths of mitotic and interphase cells in a single file are correlated. Data for the wheat root, replotted from Dobrochaev and Ivanov (2001).

of a pair of sister mitotic cells differs from unity if there were differences in either the elongation rates of the sisters, their lengths at birth, or the duration of their cell cycles. Symplastic growth ensures that any difference in elongation rate between sisters will be negligible, and proliferative cell divisions in the root are usually symmetric. In contrast to the large variation in the length of mitotic cells over a whole tissue, the average difference in length of sister mitotic cells is invariably small (Ivanov 1971; Demchenko 1975; Webster 1979; Barlow 1983; Armstrong and Francis 1985). For example, Dobrochaev and Ivanov (2001) reported the difference in length between mitotic sisters was rarely more than 10% of the sisters' mean length; similarly, the difference in length between mitotic neighbors (that is, mitotic cells in a file that are adjacent but not sisters) was also small (less than 14%). This shows that the cell cycle departs markedly from a constant duration rarely if ever among sisters or neighbors. Therefore, unless sisters and neighbors have a specific mechanism to suppress cell cycle variation, this suggests that all proliferating cells in a tissue have a similar duration of their cell cycle.

## DURATION OF THE CELL CYCLE ALONG THE MERISTEM IN VARIOUS TISSUES

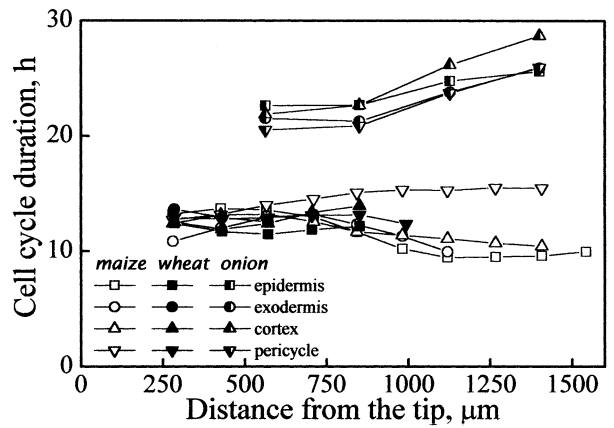
As with different positions, different tissues are widely assumed to have different cell cycle durations. This assumption may arise from tritiated-thymidine experiments, which typically report that the cell cycle varies in different tissues. The labeled-thymidine method assumes that every cell becomes appropriately labeled, an assumption that sounds reasonable but, as discussed above, is apparently false. Although these experiments may be correct in revealing variability in the cell cycle duration between tissues, it is also possible that the results are distorted by differential labeling efficiency between tissues. However, the profile of cell length, when compared between the proliferating regions of different tissues, does not support the idea that the cell cycle differs appreciably between tissues. Differences in cell length between tissues tend to remain constant as a function of position, from where the tissue forms to the location where division ends (Baskin 2000). This has been shown many times; for example, the length of metaxylem cells, over the region where they divide, stays strictly constant with position, as does the difference between their length and that of other dividing tissues (Ivanov and Maximov 1999). If there were differences in division rates between tissues, then the difference in cell length would become progressively larger under the influence of exponential division and symplastic growth. For example, assume that the cell division rate differed in two tissues by a factor of 1.15 and that, at the start of the meristem, the tissues had equal cell length: after five divisions, which is typical for transit across the meristem (Beemster and Baskin 1998), cell length between the tissues would differ by a factor of 2. To our knowledge, there are no reports of cell length progressively diverging across the proliferating zones of different tissues.

To compare cell cycle duration absolutely, as can be seen from Equation(2), in addition to cell length, one needs the relative growth rate. Although it is possible to measure the relative growth rate directly by marking the plant and making time-lapse observations, this is not always practical, and obtaining accurate growth data for the meristem is difficult because of the slow elongation rates involved. To get around this problem, authors have used the length of metaxylem cells, which stop dividing close to the quiescent center; consequently, for locations basal of the cessation of division, metaxylem cells provide a record of elongation rate as a function of



**Figure 5.** Illustration of a method used to obtain cell cycle duration when growth is at steady state. In this example, metaxylem cells ( $\blacktriangle$ ) cease division at about 300  $\mu\text{m}$  from the tip; therefore, their subsequent increase in length records the elongation behavior of the root. The growth behavior defined by the metaxylem cells can then be used to link a cell just “born” at cytokinesis ( $\circ$ ) to a cell entering mitosis ( $\square$ ). In this example, a postmitotic cell (indicated at the arrow) is linked to its subsequent length at mitosis by translating the curve of metaxylem cell length versus position (dotted line) downward until it intersects the postmitotic cell curve at the arrow. Then the length of that cell, when it divides, is found from the other intersection (that is, the dotted line and the mitotic cell length curve). Note that cell length is plotted on a logarithmic scale. Figure redrawn from Balodis and Ivanov (1970).

position (Hejnowicz and Brodzki 1960; Ivanov 1968, 1981; Carmona and Cuadrado 1986). In Figure 5, the lengths of newly born cells are plotted as open circles and the lengths of mitotic cells as open squares. A cell expands from its length at birth to its length at mitosis based on the prevailing growth rate; the growth rate is obtained based on the slope of metaxylem cell length versus position and is used to connect nascent and mitotic cells (Figure 5, dotted line). In this way, Balodis and Ivanov (1970) calculated the duration of the cell cycle for different tissues as a function of distance from the tip for



**Figure 6.** Cell cycle duration versus distance from tip for various tissues in three different species. Data span a region bounded by the terminus of the meristem and the position where metaxylem cells stop dividing, locations that differ between the three species. Data are replotted from Balodis and Ivanov (1970).

positions basal of the cessation of division in metaxylem. It was found that the average duration of the cell cycle is practically constant among various tissues of a species, although the cell cycle of the maize root’s pericycle diverged in the basal portion of the meristem (Figure 6).

## RELATIONSHIP BETWEEN CELL SIZE AND CELL CYCLE

What triggers a cell to enter M-phase? In single-celled organisms, cell size plays an important role and cells use information about their size to decide whether to halt or progress through the cycle (Coelho and Leever 2000). In the root meristem there can be no absolute requirement for cell size because cells in different tissues divide at very different average sizes. Even in a single tissue, cells in different files divide at different lengths (Dobrochaev and Ivanov 2001). Nevertheless, one may ask if cell size exerts any role at all in regulating the cell cycle. For example, when a cell divides to produce daughters of different sizes, will the larger one divide before the smaller? As cells rarely divide exactly in half, allowing a smaller-than-average cell to delay entry into mitosis would act to maintain a constant cell size, as typically seen in the root meristem. Introducing such an influence in modeling studies reproduces the observed distribution of cell lengths closely (Korn 1993; Dobrochaev and Ivanov 1999). Otherwise, some excessively long and short cells will be produced by amplification of

the length differences through successive unequal divisions.

## CONCLUSION

The plant root meristem is complex, comprising tissues whose cells differ in size, form, and metabolic properties. Nevertheless, cells of various tissues elongate at the same relative rate. We argue here that they also divide at the same frequency, indicating that both growth parameters are built into root meristem cells at a fundamental level. Differences in cell length between various tissues appear to arise at their formation, at the tissue initials, and ultimately in the seed. Near the quiescent center, typical differences in length are already present between cells of various tissues and files of the same tissue, and during subsequent growth these differences are maintained. Although the cell cycle duration may be the same for all tissues in the root, the place where division ceases is certainly different, which increases the difference in mature cell length between tissues. This points to the mechanism whereby a cell exits the cell cycle as being a fundamental regulator of meristem performance. Discovering this mechanism will be facilitated by a realistic understanding of how symplastic growth constrains the division behavior of dividing cells.

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