



# Patterns of root growth acclimation: constant processes, changing boundaries

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Plasticity, the hallmark of plant morphogenesis, extends to kinetics. To enhance acclimation, growing plant organs adeptly adjust their growth rate, up or down. In roots, rates of division and elemental expansion as well as the length of division and elongation zones are readily characterized because of their linear organization, radial symmetry, and indeterminate growth, and can be measured accurately with kinematic methods. Here, for roots, I describe key concepts from kinematics and review patterns of growth and division during acclimation. The growth rate of a root reflects the integral of elemental expansion activity over the span of the growth zone; therefore, an acclimating plant can change the rate of root growth by changing either or both the span of the growth zone or the rate of elemental expansion. The analogous dichotomy exists for cell division where the rate at which cells are produced reflects the integral of cell division rate over the span of the division zone. Surprisingly, expansion responses nearly always involve changes in the length of the growth zone. Similarly, although based on fewer data, changes in cell division rate are rare, whereas changes in meristem length are common. These patterns imply that setting the boundaries for meristem and elongation zone is the key regulatory act for root growth rate acclimation. © 2012 Wiley Periodicals, Inc.

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## INTRODUCTION

Animals are masters of motility; plants are masters of growth. Reacting to salient features of the environment whether biotic or abiotic, an animal might walk or slither, whereas a plant might grow thinner leaves or longer stems. Animals are typically stuck with a body from birth and acclimation is limited by physiology. In contrast, plants make organs continually throughout their lives, an iterative output allowing them to sidestep some physiological constraints by virtue of development. In addition to its adaptive role for the plant, this incessant growth endows Earth with gigatons of biomass, sustains food chains, and colors our planet green.

Altogether, animals move in a bewildering number of ways; nevertheless, we can find regularities by examining homology between limbs or

shared neuromuscular circuits. Likewise, the total combination of plant species and environments is uncountable, but regularities in growth processes exist. This review will consider the seedling root. The root permeates the soil to acquire water and nutrients and also to provide anchorage. Unlike that of the leaf, root growth is usually indeterminate, meaning that there is no programmed root length, and because the root grows continuously, its growth zone sampled at any time will contain the entire developmental sequence, from early to late.

As part of an acclimation response, it is common for the growth rate of a given root to increase or decrease. But which processes are changing? Root growth includes component processes, any or all of which, in principle, could change during acclimation. Surprisingly, some of these processes appear to be flexible and vary during acclimation, but others tend to be fixed. Recognizing this regularity helps us to zero in on the specific processes relevant for acclimation and also highlights the potential relevance of exceptions.

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Here, I will review patterns of root growth during various acclimation responses after first presenting a framework for understanding root growth quantitatively. Other aspects of root growth physiology (and also of leaves) have been effectively reviewed by Walter et al.<sup>32</sup>

## A PRIMER OF ROOT GROWTH

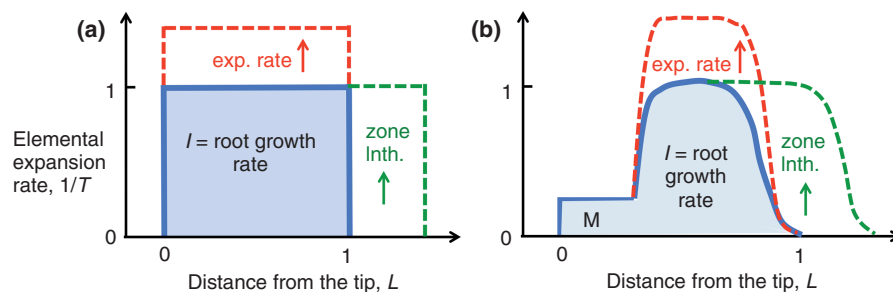
Because of their linear organization, radial symmetry, and indeterminate growth, roots make ideal subjects for investigating growth. A powerful mathematical framework was applied to root growth as far back the 1950s.<sup>10,14,16</sup> The approach is in general termed *kinematic* because it is in essence concerned with the movement of particles within the root and accounts for their motion with concepts from hydrodynamics. A formalism based on fluid flow applies well to the root growth zone (and to any plant organ) because the growth zone is continuous physically and expansion at any position causes surrounding tissue to move. Readers interested in a full account of the kinematic approach to growth, and particularly mathematical aspects, may consult the following references.<sup>11,13,15,26,27</sup> Although the kinematic framework is mature and powerful, it is seldom used; furthermore, some researchers fail to grasp certain subtle yet key features of growth zones. For both reasons, our knowledge of root growth is shallower than it could be and the literature contains dubious interpretations and outright mistakes. In this section, I will overview root growth kinematics.

In a root, the growing region is at the terminus. In zoology, it is common to describe an organ extremity (such as a fingertip) as being *distal* to the core of the body, but because this usage is not widespread in the plant literature, I will use *apical*

instead to describe the end of the root. Note that some plant cell biologists have used apical for cell polarity with reference to the shoot apex only, so that under their terminology *apical* points away from the root's apex; however, an alternative terminology for cell polarity has been recently proposed.<sup>4</sup> In any case, here, anatomy rather than cell polarity is at issue, making the organism-based *apical* and *basal* preferable terms. I will refer to the very apex of the root (a point) as the root *tip*.

Because the mature part of the root is immobilized, expansion pushes the growth zone downward, through the soil. However, the zone does not move as a unit; instead the rate of motion at any point depends on the amount of expanding material between that point and the mature, non-growing part of the root. The tip is propelled by the summed expansion over all the growing cells. This is therefore the maximal rate of motion (for that growth zone) and is the commonly measured parameter, *root growth rate*.

A summation over cells invokes a discrete (discontinuous) process; however, expansion represents deformation of the cell wall, a process that involves macromolecular components far tinier than the cell itself. On the scale of the root's complete growth zone, it is appropriate to consider expansion as continuous and the elementary unit of expansion infinitesimal. Certainly, a single cell need not have a uniform rate of expansion from one end to another. Consequently, rather than a summation, root growth rate reflects an integral. The magnitude of the integral (i.e., the rate of root growth) depends on the length of the growth zone (the amount of growing material) and the rate of the expansion process (the intensity of growth). For an idealized growth zone within which the expansion process is strictly constant from tip to base, the integral is simply the product of the length of the growth zone and the expansion rate (Figure 1(a)).



**FIGURE 1** | Hypothetical patterns of expansion within a growth zone. The units on the axes are dimensions ( $T$  = time;  $L$  = length), and a value of 1 is arbitrary. (a) Wholly idealized growth zone in which there is a uniform rate of elemental expansion (blue line). The area under the curve (light blue) equals root growth rate, easily calculated as the product of the length of the growth zone and the rate of elemental expansion (dimension of  $L/T$ ). Dashed lines show increased expansion rate (red) and increased zone length (green). (b) More realistic root growth zone, with a region corresponding to the meristem (M) and with rates of elemental expansion that vary with position. The area under the elemental expansion rate curve requires integration to calculate but still equals root growth rate. Increases in expansion rates and zone length are indicated, as in (a).

Real root growth zones are more complex. As is well known, the growing portion of the root comprises meristem and elongation zone. In the meristem, cells both divide and expand, whereas in the elongation zone, they only expand; however, the rate of expansion is roughly an order of magnitude greater than that of the meristem. Besides this large difference, the elemental rate of expansion might vary with position within each zone. While this causes difficulties for the would-be integrator, the magnitude of the integral (and hence of root growth rate) still depends on both the size of the growth zone and the rates of elemental expansion (Figure 1(b)).

This relatively straightforward mathematical relationship has the consequence that, in any acclimation, there are two ways in which a root can change its growth rate. These two ways are distinct although not exclusive. On one hand, the elemental expansion process itself can change, for example, by making cell walls looser or tighter. On the other hand, the size of the growth zone can change, becoming larger or smaller (Figure 1). Changes in elemental expansion are usually imagined, perhaps because that is what occurs in the classical physiological demonstration of adding auxin to a shoot stem segment. But clearly, doubling the length of the elongation zone without any change in expansion rate will nearly double root growth rate (not an exact doubling because the contribution to root growth rate from the meristem would not likewise be doubled). Is there any adaptive value in making one kind of change versus another? I return to this question below after considering cell division.

What about cell division? The process of cell division builds a wall between cells, an act that reduces cell volume by one half and does nothing to the volume (or length) of the root. For that reason, on a direct level, we should remember that cell division is not a growth process. The pattern of growth in Figure 1(b) is generated by local variation in cell wall production and deformation and thus could perfectly well represent a root growth zone comprising a single, enormous cell. However, plant organs are, in reality, multicellular. Along with increasing volume, growth zones are responsible for partitioning the plant body.

Cell division is distinct from expansion, but it is linked to expansion. First, the cell cycle typically has a cell-size checkpoint, so that a cell cannot divide unless it has passed a threshold size. In the plant root, the existence of such a checkpoint can be inferred because cell length within the meristem, for a given tissue and position, tends to stay constant. A constant cell length requires rates of elongation and cell division to be equal. The observed constancy of cell length reveals a

tight coupling between division and expansion, but the mechanism of the coupling has been little explored. Second, division generates cells whose subsequent fate entails a great deal of expansion. Cells produced by the meristem flow into the zone of elongation. Thus, the more cells produced by the meristem per time, the more cells can flow into the elongation zone in the same time, potentially increasing the amount of expansion. Expansion is increased *potentially* by the supply of incoming cells because those cells become subject to regulation within the elongation zone itself. All things being equal, the faster that cells flow into the elongation zone, then the more cells will be expanding at any time and hence the elongation zone will be longer and root growth rate faster. In summary, cell division is linked closely to expansion within the meristem through cell cycle regulation and is linked indirectly to expansion in the elongation zone through provisioning that zone with the raw material for expansion (i.e., cells).

Regardless of the precise relationships between division and expansion, division is interesting in its own right and worth quantifying. Notably, the issues are similar to those introduced above for expansion. Analogous to root growth rate, *cell production rate* is defined as the number of cells produced per unit time, usually calculated for a single file of cells. Cell production rate encapsulates the total proliferative performance of the meristem (or cell file thereof). Just as root growth rate depends on both the rate of elemental expansion and the length of the growth zone, so too cell production rate depends on the rate of cell division and on the number of dividing cells. These relationships can be summarized by saying that increases in both cell number and organ volume are determined by the intensity of a process (division or expansion rates) and by the span over which that process occurs (zone length or cell number).

While reports of root growth rate are common, reports of cell production rate are rare. This rarity is unfortunate because just as root growth rate shows the total expansion activity so too cell production rate shows the meristem's proliferative performance. Furthermore, cell production rate is easy to measure: it simply equals root growth rate divided by mature cell length (usually of a specific tissue, say cortex). This equivalence is strictly true only for steady-state growth, but the departure from steady state needs to be extreme before the steady-state assumption becomes problematic. As one example of the usefulness of this parameter, Beemster et al.<sup>7</sup> characterized root growth characteristics of a few dozen *Arabidopsis thaliana* accessions by measuring root growth rate, cell production rate, and estimating the number of

dividing cells; in doing so, they showed how these parameters were correlated with certain putative regulatory factors but not with others.

Just as they do for expansion, kinematic methods offer a powerful method to quantify cell division rate and its distribution within the meristem. The method relies on the so-called equation of continuity, which is a mass-balance equation, equating at a specific position, the rates of processes that produce substance X with rates of those that remove it. For the case of X being cells in a meristem, cells are produced by the act of cell division and removed both by their velocity, which literally removes them from that given position, and by expansion, which effectively dilutes their concentration. In practice, one calculates local cell division rates from the spatial profiles of velocity and cell length. Methods for making these measurements have been described comprehensively by Rymen et al.<sup>23</sup> Despite their power, kinematic methods have been applied to studies of cell division infrequently.

Finally, before turning to observations of growth acclimation, there is a further consideration. The above description is spatial. That is to say, the extent of a growth or division zone is equated to a spatial dimension (length). However, it is possible alternatively to use a temporal framework, and consider the length of time needed to traverse the zone. In visualizing the temporal framework, because the time required to traverse a meristem usually exceeds one cell cycle, transit times are best applied to a transverse cell wall or other element-like entity, rather than to a cell. The spatial scale can be transformed to a temporal scale based on the velocity profile, because it specifies the amount of time required to move between any two points in the root. In general, it will take longer to move a given distance in the meristem, where velocity is low, compared to in the elongation zone, where velocity is high. In fact, while the typical difference between meristem and elongation zone in length is about fourfold, the difference to traverse them in time is about 20-fold.

Note that, for the above transformation, the relevant velocity is with respect to the root, not the absolute velocity (i.e., with respect to the soil or growth medium). At any position,  $x$ , the root-specific velocity is equal to the difference between the absolute velocities at the tip (i.e., root growth rate) and at  $x$ . This gives a root-specific velocity equal to zero at the tip and equal to root growth rate over the entire mature zone. While it is amusing to visualize a mature root zooming up and out of the ground, using the root reference frame facilitates

the transformation between temporal and spatial scales.

Viewing the root along a temporal axis is informative, particularly where the rates of component processes are of interest; but often, the relationship between space and time is misunderstood. For example, in evaluating histological changes during an acclimation, one might see differentiated cell types closer to the tip in the treated sample, but this does not necessarily mean the timing of differentiation is changed. If the treatment changes root growth rate then the relationship between space and time will also change. A 100- $\mu\text{m}$  span of mature root corresponds to 6 min in a root growing at 1000  $\mu\text{m h}^{-1}$  and to 24 min in a root growing at 250  $\mu\text{m h}^{-1}$ . Only by making this transformation, one can evaluate whether an observed spatial change reflects changed timing in an underlying process.

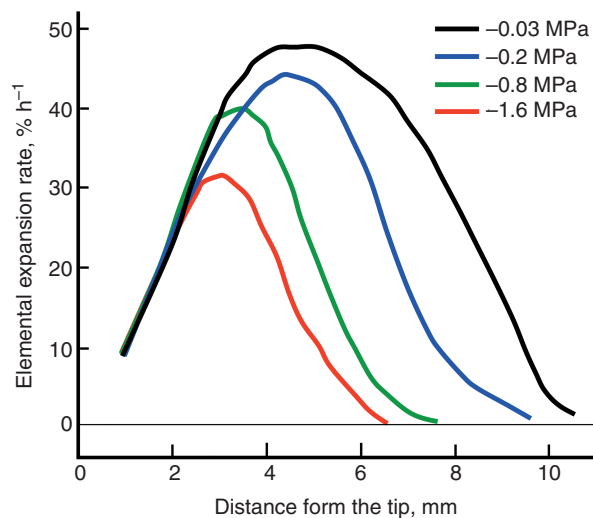
Despite the usefulness of the temporal viewpoint, the following sections will be mainly spatial. There are two reasons for this. First, while in general there have been few kinematic studies of growth patterns, even fewer of them have included temporal analysis. Second, while the provision of a velocity profile is enough for the transformation in principle, it is difficult in practice because the transformation is disproportionately affected by the low values of velocity in the meristem, which, as described more fully below, are difficult to measure.

## PATTERNS OF ROOT GROWTH ACCLIMATION: EXPANSION

When roots encounter an altered environment, they might grow slower to conserve nutrients or faster to reach new ones. Indeed, in studies of acclimation, changes in root growth rate are commonplace. How are these changes caused? On the basis of the above account, we might expect some to be driven by changes in expansion rate and others by changes in the length of the growth zone, and yet others by both kinds of changes. Altogether, the number of papers where growth parameters have been resolved spatially is still rather small; nevertheless, there are enough of them to conclude that changing the length of the growth zone, rather than changing expansion rate, is the preferred means for changing root growth rate.

The most commonly observed pattern of growth acclimation is exemplified by the maize root responding to water-deficit stress (Figure 2). When roots grow in dry vermiculite, the elongation zone is truncated apically, with the greater the water deficit, the greater the amount of truncation.<sup>25</sup> A similar





**FIGURE 2** | The commonly observed pattern of changing growth zone length. This example illustrates the response of maize roots experiencing various levels of water-deficit stress. Data were obtained 48 h after the imposition of stress when the response has essentially reached steady state. The legend refers to the water potential of the vermiculite growth medium.<sup>25</sup>

apical truncation has been seen for water-deficit stressed soybean roots.<sup>36</sup>

Besides water-deficit stress, the elongation zone is truncated apically (as in Figure 2) in response to a host of stresses, including soil compaction (pea),<sup>9</sup> osmotic stress (pine),<sup>30</sup> excess sodium (thale cress),<sup>34</sup> phosphorous deficiency (thale cress),<sup>18</sup> and sub-optimal levels of irradiance on the shoot (maize).<sup>19</sup> Likewise, the elongation zone is truncated apically when roots are exposed to sub-saturating doses of a chemical inhibitor that depolymerizes microtubules (thale cress).<sup>3</sup> The relationship between stress and the chemical removal of microtubules is not obvious, but microtubules are lost under certain stresses, such as aluminum<sup>28</sup> or cold.<sup>8</sup> Also, apical truncation of the elongation zone occurs when thale cress roots are exposed to cytokinin,<sup>6,37</sup> auxin,<sup>22</sup> ethylene,<sup>29</sup> or to 2% sucrose<sup>12</sup>; again, while the physiological significance of these treatments is ambiguous, the changed zone size is clear. Finally, the elongation zone is enlarged basally when tobacco seedlings are grown at low-light irradiance and then exposed to a higher one,<sup>20</sup> and during the development of thale cress roots as daily growth rate accelerates.<sup>5</sup>

In contrast, responses in which elemental expansion rates change while the growth zone length stays constant are rare. One of these is temperature. For maize seedlings grown at temperatures between 16 and 29°C, the bell-shaped profile of elemental expansion rate versus distance scales with temperature, with little if any concomitant change in the length of the

elongation zone.<sup>21</sup> This result has been confirmed with high-resolution image processing methods, albeit for a comparison of only two temperatures.<sup>33</sup> The pattern of the maize root's response to temperature was interpreted as signifying that a growth-limiting reaction is poorly temperature compensated.<sup>21</sup> If so, this implies that the observed pattern of response reflects a direct influence of temperature at the level of expansion mechanism as opposed to a regulated response, wherein the root senses the altered temperature and activates a program of change.

Besides the response to temperature, there are other examples of growth zone constancy, but only a few. When ethylene action is inhibited chemically in thale cress roots, the magnitude of expansion rate changes throughout the elongation zone with little change in the zone's length, and interestingly in seedlings grown under phosphorous deficiency, expansion rates go down but in phosphorous-sufficient seedlings the rates go up.<sup>18</sup> Although this is an example of constant zone length, the specificity of the inhibitor used needs to be verified before drawing too many conclusions about the role of ethylene in regulating expansion rates. A constant elongation zone length despite different root growth rates has also been found for comparisons of maize roots grown in pure water versus a complete nutrient solution<sup>31</sup> and for *Nicotiana attenuata* seedlings undergoing simulated herbivore attack.<sup>17</sup> The latter two reports establish that the root is able to regulate elemental expansion rate, but the surprising point is the rarity of such examples.

In the exemplified pattern (Figure 2), along with the changed position of the end of the growth zone, elemental expansion rates do change. Notably, the maximal expansion rate in the well watered exceeds that of the strongly water stressed. This implies that the acclimation to water stress, in addition to the boundary change, includes a mechanism specifically to decrease expansion rate. However, this need not be the case. The process of expansion rate deceleration (i.e., going from the maximum to zero) requires a finite span: in automotive terms, putting on the breaks requires a certain length of road before the car stops. Moving the boundary of the growth zone apically involves, by default, a comparable apical shift in the position where expansion rate begins to decelerate, a shift that, if large enough, will require deceleration to begin before expansion rate reaches its maximum. Thus, the decreased expansion rate maximum (as in Figure 2) could reflect an indirect consequence of the moved boundary, without a specifically programmed change in expansion rate. Again, these need not be exclusive and in general we can imagine an apical

shift being accompanied by stronger brake pads (to extend the automotive metaphor) to carry out the deceleration. Nevertheless, such an accompaniment is hypothetical, whereas the changed growth-zone boundary is observed.

Finally, in the apical part of the water-stressed root's elongation zone, expansion occurs at rates indistinguishable from those of the well-watered controls (Figure 2). This is important because with so little water available (e.g., water potential of  $-1.6$  MPa), maintaining expansion rate requires the expansion process to be adjusted substantially, in this case apparently by increasing cell wall extensibility.<sup>35</sup> Here, the unaltered expansion rate can be inferred to be deliberately achieved, as it can for many of the responses to stress cited above, insofar as they are sufficiently severe to alter physiology pervasively. Thus, the maize root stressed by water deficit sounds the leitmotif for growth acclimation: the length of the growth zone is flexible and expansion rate is maintained.

## PATTERNS OF ROOT GROWTH ACCLIMATION: CELL DIVISION

Likewise for division, acclimation could involve changing either or both the rate of cell division or the number of dividing cells (i.e., length of the meristem). Parallel to expansion, changes in apparent meristem length are widespread, but it is not known how commonly cell division rate changes because these rates have been so rarely measured.

One of the characteristics of the root of the ever popular thale cress is that the elongation zone contains relatively few cells; for this reason, cell length can be seen to increase rather abruptly at the start of the elongation zone. This allows the span of the meristem to be apprehended by eye and to be defined based on a position where cell length passes some fixed length, say  $40\text{ }\mu\text{m}$ .<sup>7</sup> Because cells that are expanding rapidly are unlikely to be able to divide, this position provides a reliable upper bound to meristem size. However, defining the basal terminus of the meristem based on cell length assumes a constant relationship between the cessation of division and the subsequent acceleration of expansion. This is possible but to the best of my knowledge hypothetical. Therefore, any definition based on cell length can be only an approximation, albeit one that plausibly indicates the underlying trend.

The literature is full of examples showing that a particular treatment changes at least the approximate length of the meristem. Indeed, such reports are almost as common as those of altered root growth rate. What is all but always missing is an account of cell

division activity. Therefore, we do not know to what extent changes in meristem size are accompanied by changes in cell division rate. In fact, a change in meristem length need not change the total output of cells *at all* if there be an opposite change in cell division rate. Although cell division rate is difficult to measure, cell production rate can be measured easily (see section *A Primer of Root Growth*). It would be helpful where this parameter to be routinely assayed in conjunction with meristem length to gauge total proliferation activity.

Similar to expansion rate, cell division rate probably varies less than is commonly imagined. Some years ago, I reviewed cell division in the root meristem and concluded that changes in the number of dividing cells (and hence in the length of the meristem) were frequent, whereas convincing reports of changes in cell division rate were rare, outside of toxic treatments, such as high doses of a heavy metal.<sup>2</sup> Since then, the conclusion remains sound, although a few examples of cell division rate change are now known. In thale cress, the meristem gains cells with time from germination and loses cells when exposed to salt stress and, in both cases, the rate of cell division stays constant.<sup>5,34</sup> However, in thale cress treated with cytokinin (zeatin), meristem size and cell division rate both decrease, and in seedlings treated with  $30\text{ nM}$  2,4-dichlorophenoxyacetic acid (2,4-D), cell division rate decreases without any detectable change in meristem size.<sup>6</sup> The latter provides an instance of altering cell production rate by means of division rate rather than meristem size; however, this too might reflect toxicity rather than regulation. Not only does a comparable dose of the native auxin, indole acetic acid, have no effect on cell production rate but also 2,4-D is a herbicide and a  $30\text{-nM}$  dose, while not lethal, considerably damages the actin cytoskeleton.<sup>22</sup>

Another example where cell division rate reportedly decreases, along with a decrease in meristem size, is the maize root responding to water deficit.<sup>24</sup> That report exemplifies a technical difficulty inherent in characterizing the meristem's expansion behavior (and hence its division behavior) from kinematics. The fundamental kinematic parameter is the profile of velocity, giving the rate at which each point within the growth zone moves. In the meristem, the absolute value of velocity is high, as that part of the root is propelled by the entire elongation zone; but, local expansion behavior is given by the gradient of velocity (i.e., the spatial derivative) and, in the meristem, because the local expansion rate is low, this gradient is gradual. Consequently, measurement approaches, be they manual or computational, that handle the large motion of the meristem resolve the

gradient poorly; whereas, those designed for small-scale motion have difficulty in the meristem because of its large, non-uniform motion. In the Sacks et al.<sup>24</sup> work, the velocity profile within the meristem was poorly resolved and hence the change in cell division rate reported might not be real.

## CONSEQUENCES FOR REGULATING ROOT GROWTH

Despite the widespread use of roots as experimental material and despite the widespread recognition of expansion and division as bedrock physiology, we are surprisingly ignorant of how these processes are regulated. As I have reviewed here, a key mode of regulation appears to be the length of zones over which division and expansion occur. This calls our attention to three boundaries: where the zone of elongation begins, where it ends, and where cell division ends.

Flexibility of zone length and the maintenance of rate occur with sufficient frequency that I hypothesize it to be adaptive rather than coincidental. This hypothesis can accommodate cases where specific mechanisms are deployed at the base of the elongation zone to decelerate expansion. Keeping division and expansion running each at a constant rate might benefit metabolic homeostasis. Both division and expansion consume considerable energy and are interwoven with all other cellular activities. Changing the rates of these system-level processes might entail unwanted changes in the rates of other linked activities. In contrast, changing the zone length involves addition or subtraction of cells but each cell carries out the canonical program. Paradoxically, such wholesale changes to the plant body might be easier to control than tinkering with the

clockwork comprising the mechanisms for division and expansion.

How are the boundaries to the zones sited? Many conditions are known that will make a zone become longer or shorter, so we may say that protein x or hormone y is ‘involved’ in setting the length of the zone. However, recognizing involvement does not delineate a mechanism. Indeed, it is not even clear whether the boundaries are set by the root as a whole (emergent property of the system) or instead reflect cell autonomous behavior (e.g., each cell carrying out the same program with finite resources). Recently, the latter has been supported by Band et al., who hypothesize that the basal terminus of the elongation zone occurs when expansion dilutes the cellular concentration of gibberellin below a threshold level.<sup>1</sup> This hypothesis is elegant, linking growth cessation to the past history of elongation, and is supported experimentally. It remains a challenge for the future to determine its validity, as well as to discover what determines where the elongation zone starts and what determines where the meristem will end.

## CONCLUSION

‘Good fences make good neighbors’ according to proverb, and this appears to hold not only for the crotchety farmer in Robert Frost’s poem<sup>38</sup> but also for the plant root in managing the performance of its meristem and elongation zone. The challenge for the developmental biologist is to find out what are the plans and surveying tools used by the plant to build these fences, these fundamental partitions traversed by cells and setting the output levels of cell production and organ expansion.

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