

## The growth of root cells as the function of time and their position in the root

BY

Z. HEJNOWICZ and P. BRODZKI

There are two closely associated aspects of the elongation of the root: the time course of elongation of its constituent cells and the spatial pattern of the elongation rate or growth distribution in the root. For, obviously, a given course of cell elongation must be associated with a definite growth distribution. However, these associations have not been studied either empirically or theoretically. Brumfield's (1942) work has been the only exception in this regard. He studied the distribution of growth in the apex from data referring to the course of cell growth in the root, but some of his conclusions have been since found unsatisfactory (Hejnowicz 1956). On the other hand, our knowledge about each of these two aspects separately is quite extensive.

The information about the course of cell elongation in roots we owe mainly to Burström's work (cf. review by Burström, 1957). That worker has elaborated a special method which deserves to be considered more closely. The method is based on the assumption that the growth history of the particular cells is recurrent in the statistical sense. This is illustrated in fig. 1. The assumption is undoubtedly justified for roots growing at a uniform rate and characterized by the stability of cell arrangements. From the assumption it follows that the length of the successive cells, each more distant from tip than the preceding one, corresponds to the lengths of one cell measured at equal time intervals. Burström's method consists in that the curve of the dependence of the cell length on time is constructed from length measurements of epidermal cells. For the purpose the lengths of the successive cells in a file are plotted against their consecutive numbers. The time corresponding to one number for the particular type of cells, i. e. the time necessary for the displacement of one cell into the place of the next one, is computed from the average length of the mature (non elongating) cells and the elongation rate of the root. Dividing the full length of cells by the root

elongation rate the desired time for the given type of cells is obtained. The following data are thus necessary for applying Burström's method: the length of successive cells in the investigated kind of tissue, e. g. the epidermis, from the end of the cell division zone to the non-elongating cells inclusive, and the elongation rate of the root.

The results of Burström's investigations on the course of cell elongation in roots of wheat grown in the usual nutrient may be summarized by the graph in fig. 2. As is to be seen a cell which has passed

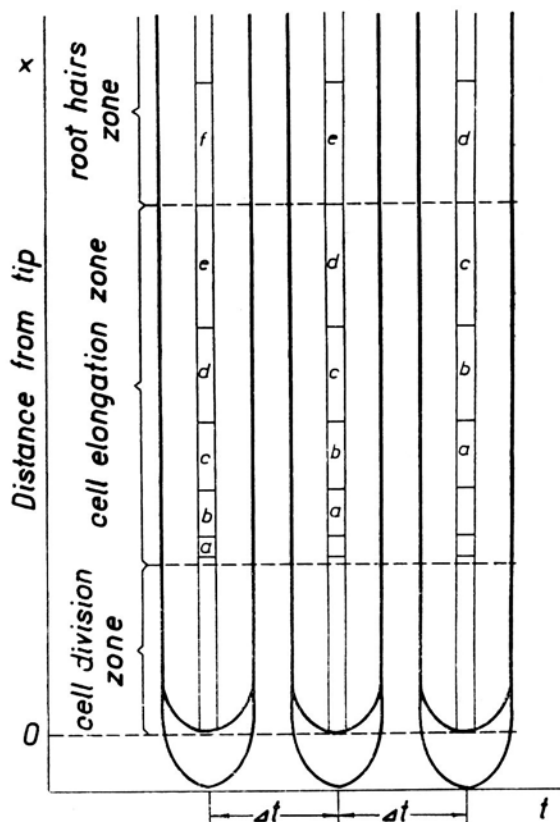


Fig. 1. The root (scheme) with a single file of cells photographed at equal intervals of time  $\Delta t$ . The length of cells in the file is a definite function of the distance from the tip. Thus, the lengths of one cell in successive equal intervals of time  $\Delta t$  are the same as the lengths of successive cells in the file

from the cell division zone to the elongation zone elongates with an increasing, or at least a constant rate until its elongation is suddenly stopped.

The other aspect of root elongation — the distribution of growth — has been more recently studied by Goodwin et al. (1945, 1956), Erickson et al. (1951, 1956), and Hejnowicz (1956). In these investigations the displacement rate method was applied. It consists in measuring, either by direct microscopic observations (Goodwin et al. 1945, Hejnowicz 1956) or by photographic techniques (Goodwin et al. 1956, Erickson et al. 1951, 1956), the rate at which artificial or natural marks on the root move away from the tip. The graph illustrating the dependence of the displacement rate of points on the distance from the tip (fig. 3) is of fundamental significance for this method. It reflects the distribution of growth, since the inclination of the curve is proportional to the elongation rate in the corresponding sections of the apex. However, a more exact characteristic of growth distribution is provided

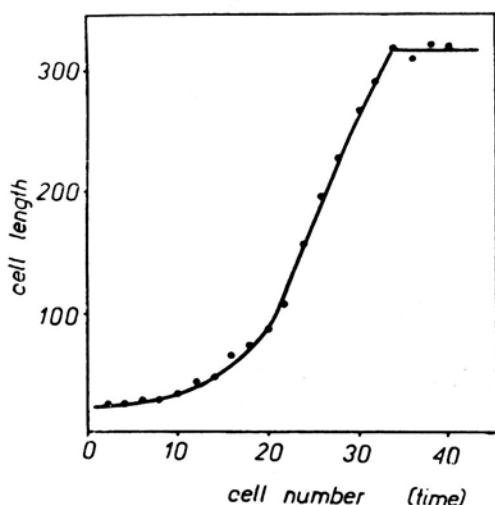


Fig. 2. The elongation curve of root cells according to Burström (1953)

by the first derivative of the displacement rate. The multiplying of the derivative by 100 gives the relative rate of elongation at a given distance from the tip in percentages per unit of time. E. g. when at the distance  $x$  the relative elongation rate is 40 per cent the cell situated at that point elongates by 40 per cent of its length in a unit of time.

The results available so far from experiments on growth distribution in roots obtained by means of the displacement method are illustrated in a general manner by the graph in Fig. 3. The relative rate of elongation expressed in percentages is constant in the cell division zone (Hejnowicz 1959). In the elongation zone the relative elongation rate rises at first and then drops as the distance from the tip increases.

Investigations on the changes of growth distribution under the influence of various factors have much significance for understanding the mechanism underlying these changes. For this reason a good knowledge of the growth distribution in normal roots is very important. It also is important for calculating the dynamics of various processes taking place in the apex (Erickson et al. 1951, 1956 b. Hejnowicz 1959).

The researches on the distribution of growth in the root and the course of elongation of root cells discussed above cover various species grown under different conditions. It is thus impossible to presume unconditionally that the course of cell elongation observed by Burström corresponds to the growth distribution reported by other workers (see

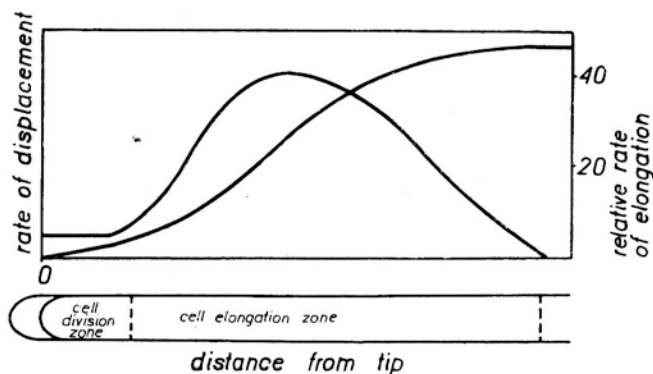


Fig. 3. Generalization of data on growth distribution in roots

Burström, 1957b). In these circumstances the aim of the present work has been to determine the distribution of growth in the root and the course of cell elongation on a comparable material.

For the experiments the rapidly growing roots of young wheat seedlings were chosen. Burström's method and a new variant of the displacement rate method were applied.

Burström's method was changed only in that the length was measured not of epidermal cells but of cortical cells and metaxylem mother cells from the central file. The measurements were made on microtomic sections. The new variant of the displacement rate method differed from the original procedure in that the displacement rate was estimated on basis of cell length measured, similarly as in Burström's method, on sectioned material. These methodic alterations were based on the reasoning that since the cell length is a function of the distance from the tip, as shown in fig. 1, the displacement rate of the transversal cell walls at various distances from the tip has to be proportional to the length of these cells. Indeed, during the time interval  $\Delta t$  the apical transversal walls of a given type of cells situated outside the cell division

zone must be displaced on the average over a distance equal to the length of the cells. When the rate of the root elongation is known the displacement rate of the transversal walls of cells which have already left the elongation zone can be calculated in absolute units. The displacement rate at any point of the elongation zone can subsequently be calculated from the aforesaid proportionality between the displacement rate of cell walls and the length of cells. It is, thus, possible to determine the distribution of growth from the same data as the time course of cell elongation which makes the comparison of the two aspects of root growth all the more reliable.

#### MATERIAL AND METHODS

The investigations were carried out on the primary and the first two adventitious roots of intact seedlings of wheat var. *Eroica Weibull's*. Soaked seeds were germinated on gauze stretched tightly over shallow dishes in such a way that the edges of the gauze dipped in water on all sides. On the second day after germination the seedlings were planted into nontranslucent holders of a culture vessel shadowed with black paper. The vessel contained 300 c. c. of the following nutrient solution:  $\text{KNO}_3$   $10^{-3}\text{M}$ ,  $\text{Ca}(\text{NO}_3)_2$   $2.10^{-3}\text{M}$ ,  $\text{KH}_2\text{PO}_4$   $10^{-3}\text{M}$ ,  $\text{Na}_2\text{HPO}_4$   $2.5.10^{-4}\text{M}$ ,  $\text{MgSO}_4$   $5.10^{-4}\text{M}$ ,  $\text{MnSO}_4$   $2.10^{-5}\text{M}$ , Fe-verseenate  $2.10^{-5}\text{M}$ . The nutrient was amply aerated by bubbling air. The vessel was kept in a climate chamber at  $25^\circ\text{C}$  under continuous light from an incandescent lamp. On the second day after planting when the length of the roots was about 35 mm. the roots of 30 plants were measured, the primary and adventitious roots separately. The culture with the remaining 30 seedlings was kept under unchanged conditions for another 13 hours, when the length of roots reached about 50 mm. The roots were then measured again and their apices, about 8 mm. long, were fixed in Cr-A-F solution. In this way the elongation rate of the roots was determined and at the same time fixed material for further examinations was obtained.

The general traits of the fixed roots were as follows: the average growth rate of the primary and adventitious roots during the 13 hours before fixing was 1.29 and 1.30 respectively and their average length at the time of fixing was 52 and 46 mm. respectively, whereas the root hairs zone started about 5 mm. from the tip.

In a separate experimental series it was found that during the 24 hours preceding and 48 hours following the phase of growth at which the roots were fixed the average elongation rate of roots was constant.

The fixed root tips were transferred to paraffin through tertiary butyl alcohol. The apices were cut on a rotating microtome into series of longitudinal sections  $10\mu$  thick. The sections were stained with tanin +

$\text{FeCl}_3$ . The length of cells was measured in the second and third layer of the cortex, counting from the outside, and in the central file of metaxylem mother cells. Drawings of the cortical layers from 6 sections from each root were made by means of projection taking for the purpose every third section from the middle of a series. The drawings covered the border between the root cap and the central portion of the root meristem, called in the course of this work the tip. They also show the transversal and longitudinal cell walls in the examined layers outside the cell division zone in these layers. In the case of cortical layers all the sections from one root were drawn on one sheet. On the other hand, one sheet was used for drawing all the files of metaxylem mother cells from one series of roots. The drawings on one sheet were arranged parallelly to each other and their apical points were placed along a straight „starting“ line. Lines parallel to the „starting“ line divided a sheet into zones of the following widths in the scale of the root (mm): 0.1, 0.1, 0.1, 0.15, 0.2, 0.3, 0.3, 0.4, 0.5, 0.6, 0.6, 0.6, 0.6, and 0.6 for metaxylem mother cells and 0.2, 0.2, 0.3, 0.4, 0.4, 0.4, 0.4, 0.4, 0.4, 0.4, 0.4, 0.4, 0.4, and 0.4 for cortical cells. The first zone became noticeable 0.46 mm. from the tip on sheets showing metaxylem mother cells and 0.92 mm. from the tip on sheets with cortical cells. Using a measure with a suitable scale the total length of all cells in a zone was determined and from the total number of cells in the zone the average length of one cell for that zone was calculated. The length of a zone divided by the average length of the cells gave the average number of cells in the zone and also the consecutive number of the middle cell in the zone. The cortical cell one mm. and the metaxylem cell 0.5 mm. away from the tip were each marked no 0.

The average length of cortical cells was established from a series of 6 primary roots or 10 adventitious roots, and the average length of metaxylem cells from a series of 10 primary or 10 adventitious roots.

The measured lengths of cell were corrected for shrinkage caused by fixation and other treatments necessary to prepare sections: the lengths of cells measured in sections was increased 14 per cent in the zone ranging 0—2 mm., 8 per cent in the zone ranging 2—3 mm. and 5 per cent in the zone above 3 mm. These corrections were based on the results of an earlier investigation on shrinkage (Hejnowicz 1959).

The shape of the curves illustrating the length of cells is of decisive significance for the present work. It is to be stressed that details of the shape of the curve are difficult to analyse statistically. However, since this work must be based on „average“ curves for series of roots some information is necessary about their statistical value. It seems that the best way of checking the correctness of an „average“ curve is to compare

it with the curves for the particular roots of the series. Consequently besides the „average“ curve for primary roots also curves for the particular primary roots were plotted.

The interpolations of the curves were made graphically, off hand. When plotting the curves inbetween the points no pre-assumed shape was followed. This method of interpolation seems to be better than mathematical interpolation in which a certain definite character of the function is preassumed. The derivatives were computed graphically.

## RESULTS

### Distribution of growth

An analysis of growth distribution based on measurements of cell lengths is possible only in that part of the root where no cell divisions take place, i.e. for cortical and metaxylem mother cells at distances from the tip of not less than 0.9 mm. and 0.4 mm. respectively.

One of the reasons why metaxylem mother cells have been chosen for observation is that their division stops when the cells are still within the general cell division zone. Owing to this circumstance the observations could be extended well into the general cell division zone. The dependence of the length of cortical cells with the correction for shrinkage on their distance from the tip is shown in fig. 4. As is to be seen the length of cells increases gradually until the distance from the tip is about 5 mm. The beginning of the horizontal section of the curve, which marks the basal boundary of the elongation zone, corresponds to the beginning of the root hairs zone.

The curves in figure 4 are based on average values calculated for series of roots. To find whether such „average“ curves adequately represent the true state of things in individual roots curves for cell length in the particular primary roots from the series have been plotted in figure 5. The shape of all these individual curves is on the whole similar and resembles the shape of the average curve in fig. 4. The particular roots differ by the length of the elongation zone and the final length of cells. The curves representing the cell lengths as the function of the distance from the tip are equivalent in their shape to the curves of the displacement rate of points, since the average length of cells at certain distance from the tip is proportional to the displacement rate of point at that distance. Thus, a different interpretation of fig. 4 and 5 is also possible: they may be regarded as illustrating the displacement rate of points. In order to represent the displacement rate in any desired

units, e.g. in millimetres per hour, it is enough to know what is the rate of root elongation, because the displacement rate corresponding to the final length of cells equals the rate of root elongation.

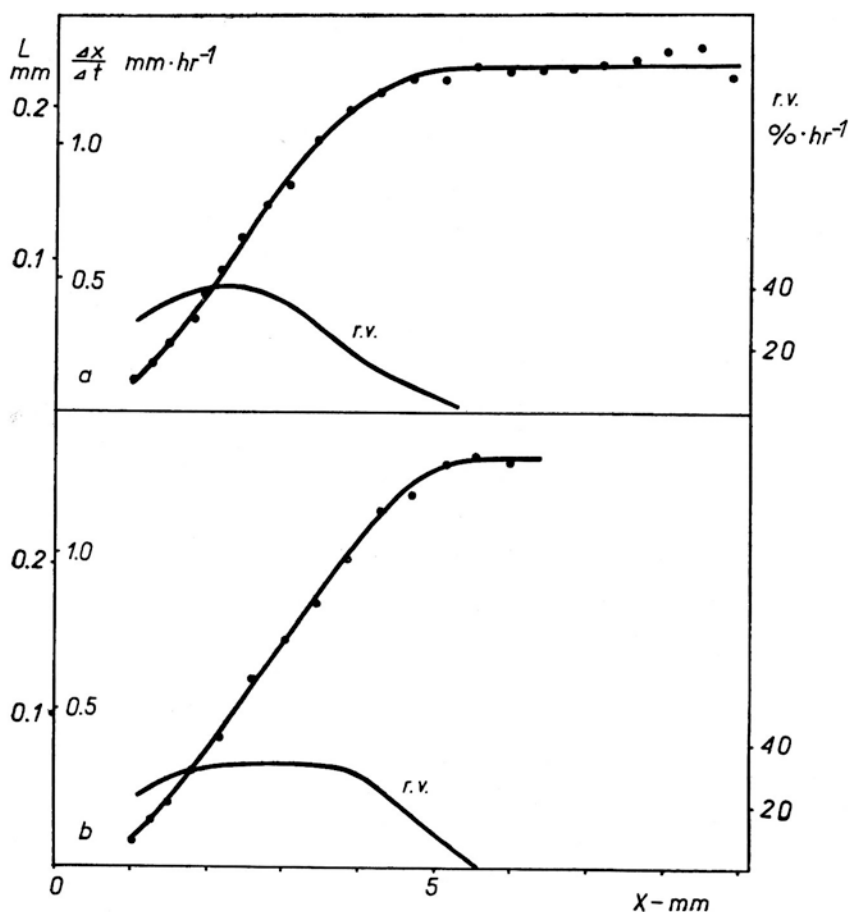


Fig. 4. The length of cortical cells plotted as the function of their distance from the tip (upper curve). The units of length are marked on the left side of the left vertical axis. The cell length curve can be interpreted as the curve of the displacement rate of points. For this purpose the calculated units of the displacement rate are marked on the right side of the left vertical axis. The lower curve reflects the relative elongation rate (*r. v.*): *a* — series of primary roots; *b* — series of adventitious roots

Since the average rate of root elongation was known it has been possible to calculate the displacement rate for the „average“ curves. The units of elongation rate determined in this manner are marked on the right side of the left vertical axis in fig. 4.

On the other hand, the elongation rate of the particular roots was not known. In this case, therefore, no determinations have been made of the displacement rate in absolute units. Thus, in the second interpretation the curves in fig. 5 reflect the rate of displacement in undefined units.

As has been already mentioned the derivative with regard to the distance from the tip of the displacement rate, plotted as the function of

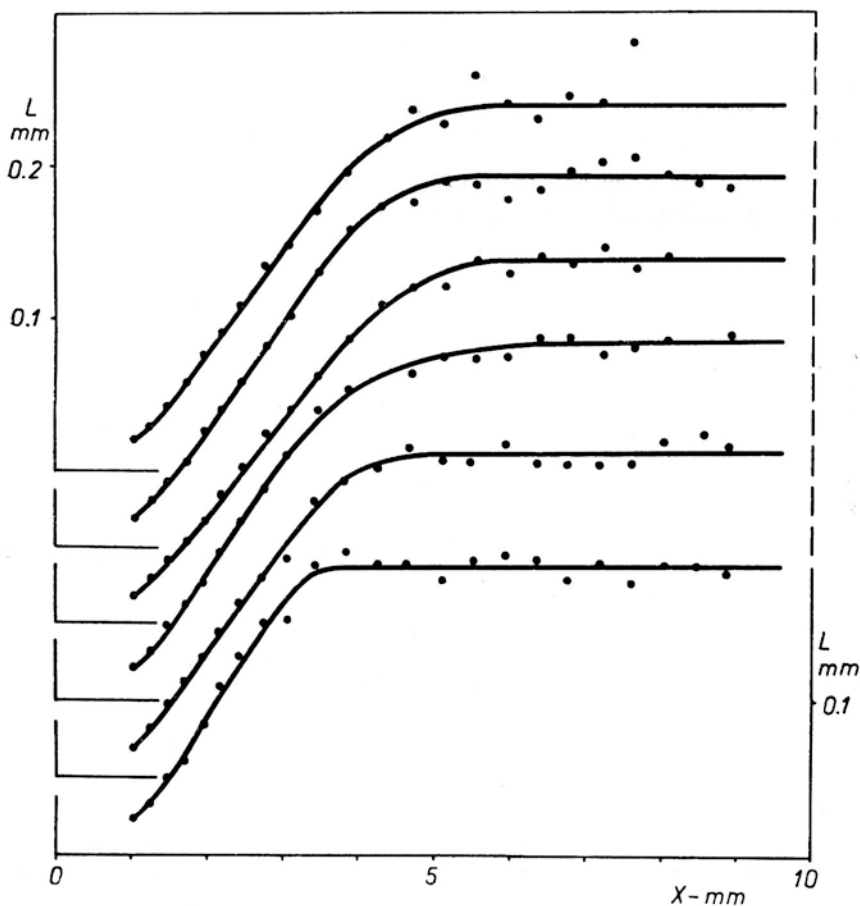


Fig. 5. The length of cortical cells plotted as the function of their distance from the tip for the particular primary roots

that distance, equals the relative displacement rate. Such derivatives have been determined from both the „average“ curves provided with defined units of the displacement rate (lower curve in fig. 4) and the curves for individual roots (fig. 6) without defined units of the displace-

ment rate. Obviously, in the former instance the relative elongation rate is in percentages per hour, whereas in the latter in percentages to some undefined unit of time.

The curves of the relative elongation rate in fig. 4 and 6 are mutually complementary. The ones in fig. 4 inform about the general distribution of growth and about the magnitude of the growth, whereas those in fig. 6 reflect the variations between roots with regard to the shape of the curves of the relative elongation rate.

As is to be seen the maximum of the elongation rate is wide in all cases. The maximum rate of elongation is about 40 per cent per hour. The rate at which the curve drops on the basal side of the maximum depends on the length of the elongation zone; when roots have a longer elongation zone the decrease of the elongation rate is slower and spreads over a longer section of the root. In roots with a shorter elongation zone

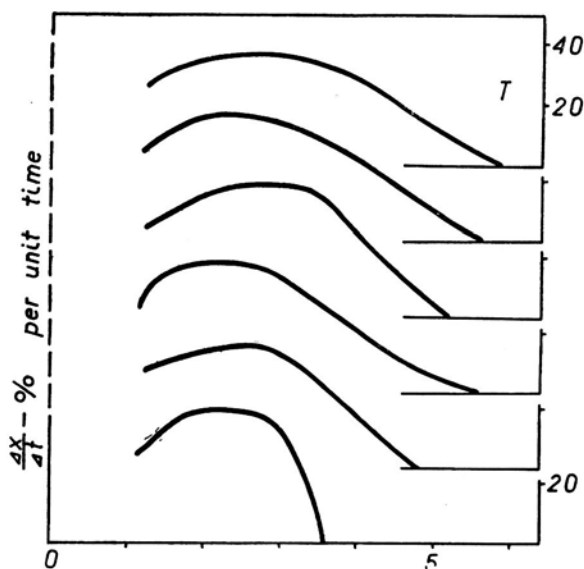


Fig. 6. Derivatives of the curves in fig. 5 complementary in their shape with the curves of the relative elongation in the particular roots

the decrease is more rapid. The shortening of the elongation zone seems to consist in the cutting away of the basal part of the zone without affecting the remaining parts. In the graphs discussed above, plotted for the cortex, the curves begin just outside the cell division zone at a distance of about one mm. from the tip. Even at that distance the relative rate of elongation is high approaching the maximum.

The analogical curves for metaxylem mother cells are shown in fig. 7 and 8. As is to be seen the curves derived from the lengths of metaxylem mother cells are similar to the ones obtained for cortical cells. They introduce no new data on the elongation zone, but partly fill the gap in the information about the apical part of the apex. The relative elongation rate (fig. 7) less than 0.9 mm. away from the tip, i.e. still within the general

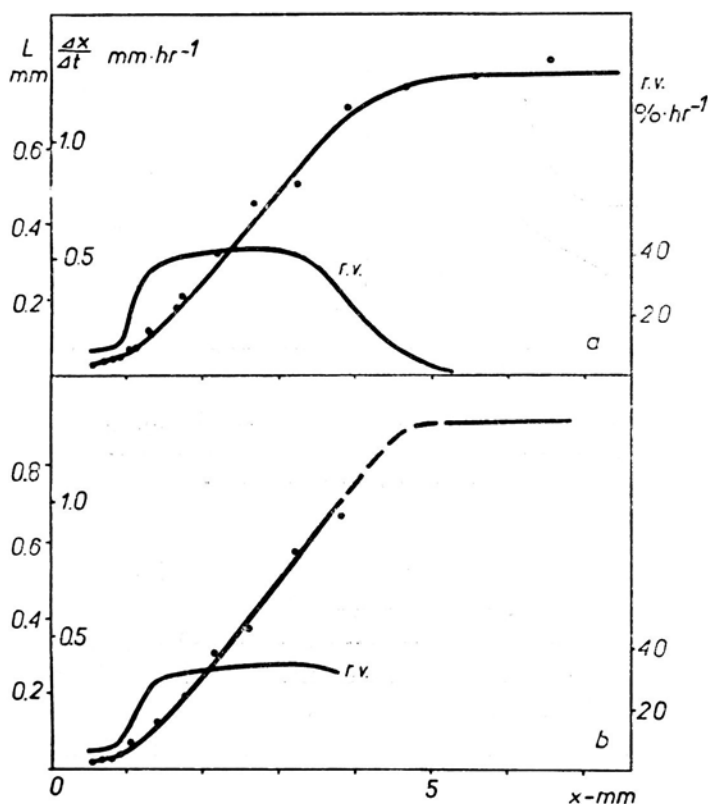


Fig. 7. The same as fig. 4 but for metaxylem mother cells: *a* — series of primary roots; *b* — series of adventitious roots

cell division zone of the root, is low but remains constant. Its sudden increase takes place at the end of the cell division zone, i.e. at the distance of about 0.9 mm. from the tip. To bring out more forcibly the uniformity of the relative elongation rate within the general cell division zone a magnified section from the apical part of the curve reflecting the length of metaxylem mother cells is shown in fig. 8. In the section from 0.5 to 0.9 mm. the lengths of these cells are arranged linearly. This means that

in this section the rate of displacement changes linearly along the straight line; the prolongation of the line stretches approximately to the tip of the root. Thus, the relative rate of elongation in the zone of cell division must be constant.

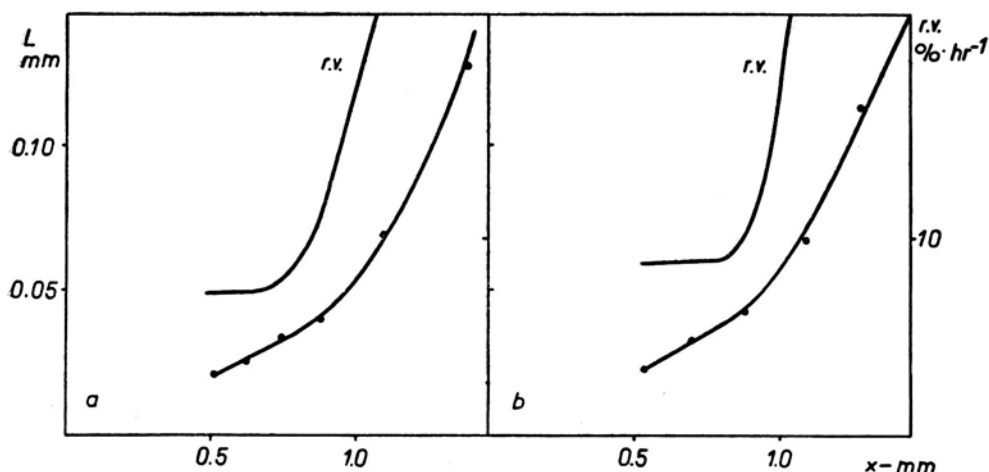


Fig. 8. Fragments of the curve in fig. 7 magnified. The length of metaxylem mother cells in the apical part of the root and the calculated from it relative elongation rate in that part of the root

Summarizing, it can be stated that the following zones of growth can be distinguished in the root apex of wheat:

- 1) the zone of slow elongation corresponding to the cell division zone,
- 2) a rather narrow zone of sudden increase of the elongation rate at the end of cell division zone,
- 3) a wide zone of rapid elongation with weakly marked maximum in the middle, and
- 4) a zone where the rate of elongation decreases gradually; the length of this zone may differ in various roots.

#### The course of cell elongation

The length of cells, taking into account the correction for shrinkage, is shown in figs. 9, 10, and 11 as the function of their consecutive number, and thus as the function of time. The cell numbers and the time are marked on the horizontal axes of the graphs, the cell number at the top. The cortical cells and metaxylem mother cells marked no. 0 are those

situated at the distance of respectively 1 and 0.5 mm. from the tip. The axes of time are at the bottom of the graphs, the time corresponding to one cell number has been calculated from the average length of no-

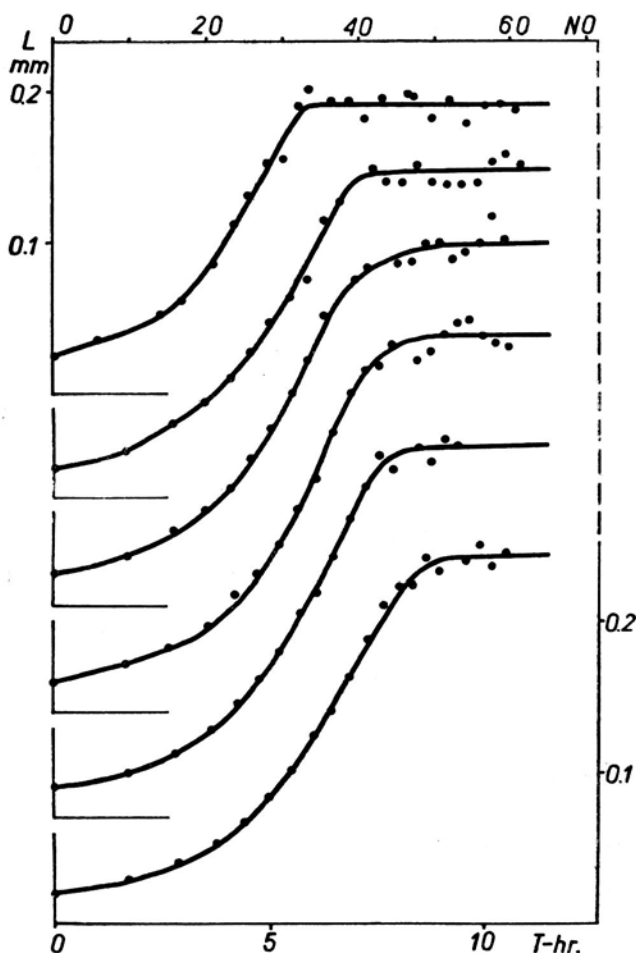


Fig. 9. The length of cortical cells plotted as the function of the consecutive cell numbers (horizontal axis at top of graph) and, thus, also as the function of the time (horizontal axis at bottom of graph). Number 0 (time 0) has been assigned to the cell one mm. away from the apex. The particular curves correspond to single primary roots

elongating cells and the average elongation rate of the roots in the series. The time calculated in this way is marked on the „average“ graphs for root series as well as on graphs of the particular roots. In the latter

case the cell numbers should have been transformed into time from the final length of cells and the elongation rate of each root separately. However, the error caused by substituting the average for the individual data seems to be insignificant, in spite of some differences between the final lengths of cells in the particular roots. This is supported by the author's own observations which indicate that the final lengths of cells differ parallelly to the differences in the rate of cell elongation, and the quotient of these two values, giving the value  $\Delta t$  for one cell number, is more or less stable under the same conditions of growth.

The curves illustrating the dependence of cell length on the cell number, i.e. on time, resemble the curves obtained by Burström (1953). The increase of the cell length slow at first, then more and more rapid,

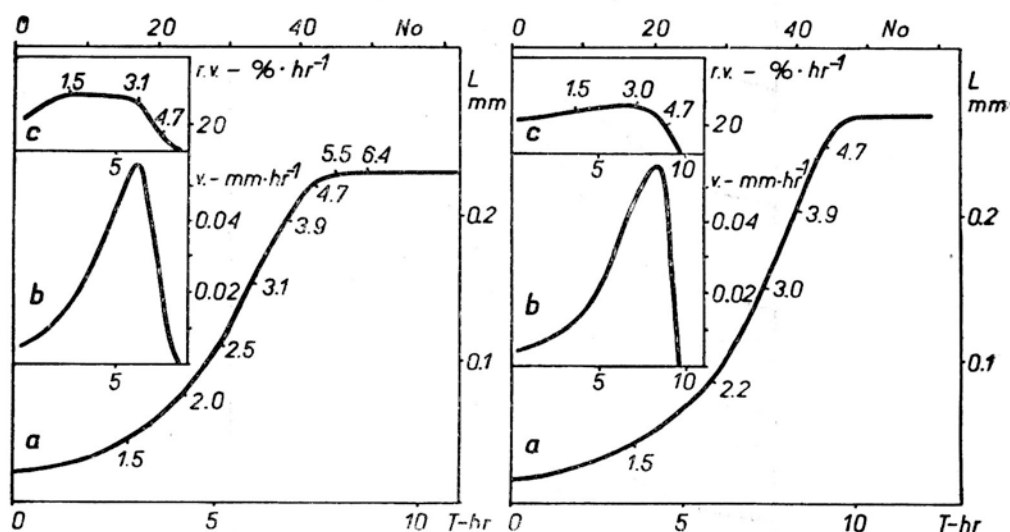


Fig. 10. Curves for series of roots plotted from the lengths of cortical cells. Right — for series of primary roots, left — for series of adventitious roots: a — length of cells as the function of time (of cell number); b — absolute growth rate of cells; c — relative growth rate of cells

finally stops suddenly within a short time. When the results for the roots from one series are compared it is to be seen that the course of growth is similar in all the roots from the series, though there may be some differences in the time that elongation from the initial to the final length lasts.

The shape of the interpolated curves has much significance for the present considerations. Among the more interesting details of the curves are those which are associated with the retardation of cell growth. Burström (1953) suggests that there may be factors which suddenly

stop the elongation running at its maximum rate. This would be reflected by a sharp bend in the curve of the function  $1 = f(t)$ . On the other hand, it is to be stressed that such a detail in the shape of the curve lies within the limits of statistical error. Without answering the question whether the retardation is sudden or not, the curves in figs. 9, 10 and 11 show that the retardation of growth takes place in a rather short time.

The curve of cell elongation, at the time of the most intense elongation, may appear at first sight to run along a straight line. In other words, it may seem that the elongation rate in that phase is constant. However,

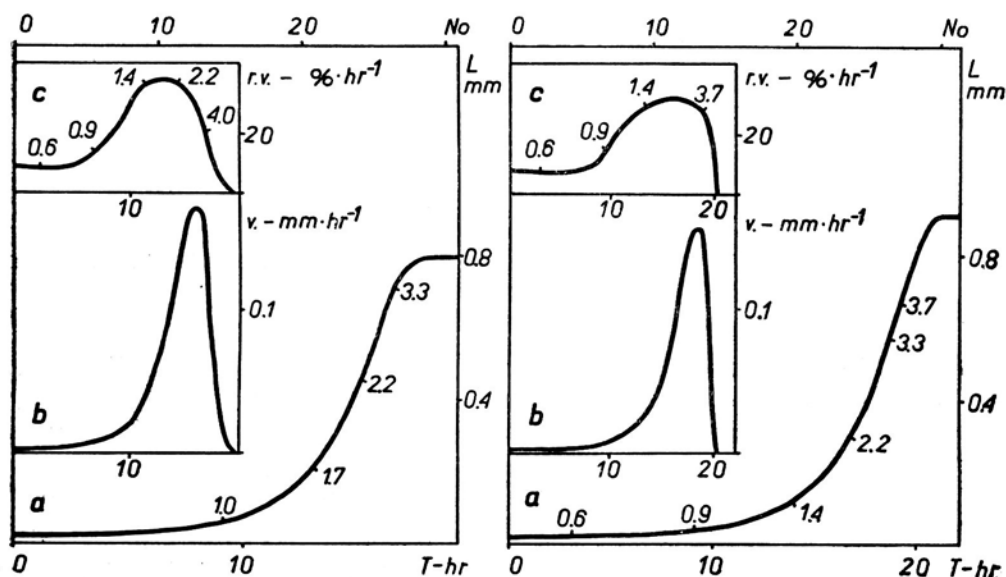


Fig. 11. The same as fig. 10 but for metaxylem mother cells

calculations of the elongation rate of cells at various moments show that the rate changes continuously. The cell elongation rate, i.e. the ratio of the increment of cell length to the increment of time, can be calculated as the tangent slope of the cell elongation curve. The values of the elongation rate are shown by curves *b* in fig. 10 and 11.

As is to be seen the elongation rate of cells increases with time till it reaches a high maximum and then in a short time drops to nought. Another thing apparent from the curves is that the elongation of cells does not fully comply with the grand period of growth proceeding at a gradually decreasing rate after the maximum is passed. This is in agreement with Burström's results.

When the elongation rate of a cell is divided by its length the relative elongation rate is obtained; its values are shown by the curves *c* in fig. 10 and 11. The relative elongation rate of cells varies within narrow limits over a long period of time from the moment a cell leaves the cell division zone till it almost reaches its final length. This means that the newly formed parts of the cell wall acquire similar growth properties as the properties of the parts formed initially. The same conclusions are

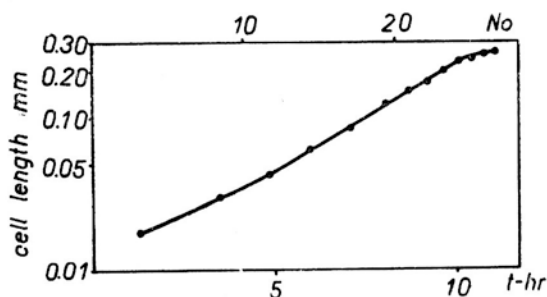


Fig. 12. Logarithms of cell lengths of cortical cells plotted as the function of time for the series of adventitious roots

arrived at by analysing the dependence of the logarithm of the cell length on time (fig. 12). The logarithmic curve forms a straight line from the time that a cell enters the elongation zone almost to the end of elongation when in a short time swings to the horizontal. The curve closely resembles the one obtained by Brumfield (1942) in his experiments on the *Phleum* root. The proportionality of  $\log_1$  to time means that the coefficient of the relative rate of growth is constant over that period of time.

#### Comparison of the growth distribution and the course of cell elongation

The curves reflecting the distribution of growth and the course of cell elongation discussed above refer to the same plant material. Even the initial data used for plotting them are the same. Thus, the distribution of growth illustrated by the curves in figs. 4, 6 and 7 corresponds to the course of cell growth illustrated by the curves in figs. 9, 10 and 11.

One noteworthy problem comes up when these results are compared: the retardation of cell elongation spreads over a rather long section of the root, though it lasts a rather short time. The reason is that a cell is displaced away from the tip at an increasing rate as the distance from the tip becomes greater. As is to be seen from the figures marking the

curves *a* and *c* figs. 10 and 11 a cell remains in the 1—3 mm. zone for 6—7 hours, whereas in the 3—6 mm. zone for 2 hours only. The metaxylem mother cells remain in the 0.5 mm. long section of the cell division zone, when their division has already stopped, just as long as they remain later in the 4 mm. long elongation zone.

It is to be noted that the distribution of growth determined in the course of the present investigation on the roots of wheat is essentially in agreement with the distribution of growth reported for various species by Goodwin and Avers (1956), Erickson and Sax (1956), and Hejnowicz (1956). Nevertheless, there are some differences

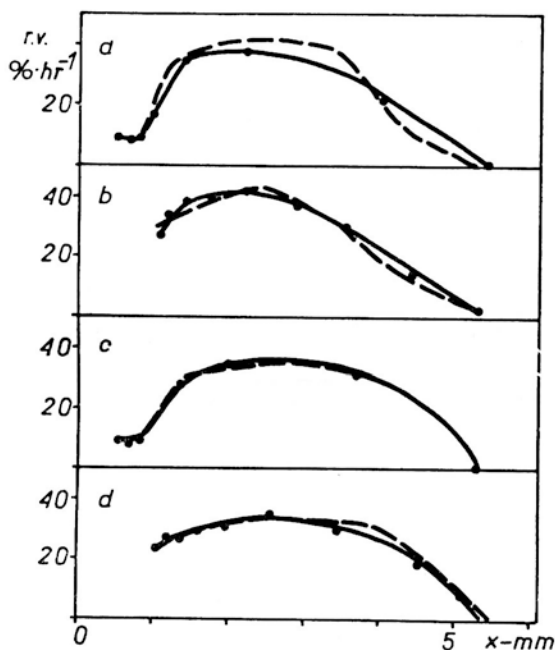


Fig. 13. Relative cell elongation rate plotted as the function of the distance from tip (see text). *a*, *b* — series of primary roots; *c*, *d* — series of adventitious roots; *a*, *c* — metaxylem mother cells; *b*, *d* — cortical cells

between the results of these workers in the shape of curves illustrating the relative rate of elongation: the curves now obtained have a flatter and wider maximum of elongation rate. On the other hand, worth noting is the concurrence of the various results with regard to the retardation of growth spread over a rather long section of the root, though as has been demonstrated in the present experiments, the length of the retardation zone may differ in various roots.

In an earlier investigation (Hejnowicz 1959) on the elongation rate in the apical part of the root this author found that the relative rate of elongation in the general elongation zone was constant. The same is indicated by the analysis in the present work of the elongation rate in the basal part of the cell division zone based on the lengths of metaxylem mother cells.

This result is highly significant. At this point apparent differences arise between the results of this author and of Goodwin and Erickson who state that also in the cell division zone the elongation rate gradually increases with the distance from the tip. The reason for the apparent discrepancy was explained in the earlier paper of the present author and

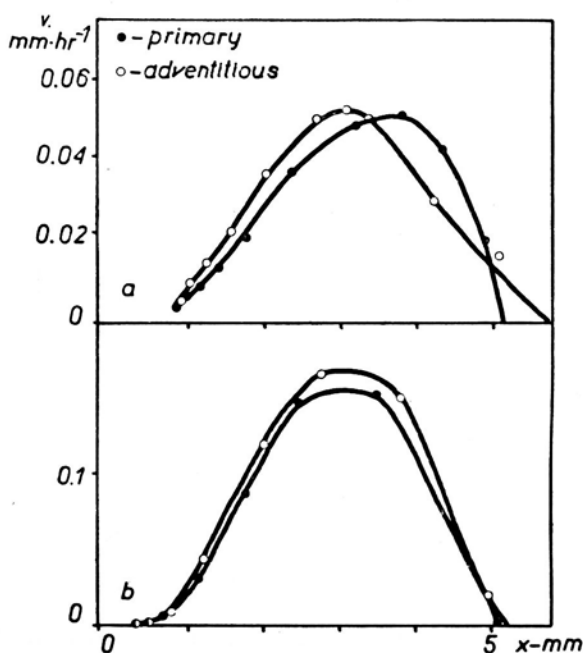


Fig. 14. Absolute elongation rate of cells as the function of their distance from the tip. *a* — cortical cells; *b* — metaxylem mother cells

the conclusion then reached was that the evidence in favour of the constant elongation rate in the cell division zone is more convincing.

Another interesting point is the concurrence between the value of the maximum relative elongation rate established by this author and by other workers. Under optimum conditions for the growth of roots the maximum is in all instances about 40 per cent per hour.

On the other hand, the course of cell elongation here described closely resembles the course reported by Burström. Thus, the course of cell elongation observed by Burström corresponds on the whole to the growth distribution described by Goodwin and Erickson.

When the position of a cell at various moments during its elongation is known, the relative elongation rate of cells may be expressed as the function of the distance from the tip. To enable these calculations the curves in figs. 10 and 11 have been supplied with figures indicating the position of cell. The distribution of growth determined in this indirect manner is shown by the curves in fig 13, where for comparison the growth distribution curves determined directly (dashed lines) are also plotted. As is to be seen the concurrence between the two kind of curves is almost complete. Thus, the statement that the curves illustrating the course of cell elongation and the distribution of growth are conformable is supported once again.

In connection with the problem under consideration attention should be drawn also to the rate of cell elongation in various parts of apex. The starting point in this case are the curves *b* in figs. 10 and 11, whereas the relevant curves are plotted in fig. 14. As is to be seen the maximum of the cell elongation rate is situated in the middle of the elongation zone. On the other hand, the elongation rate of cells when they are still in the cell division zone is very small, which is revealed by the curves for metaxylem mother cells. It is to be noted that this kind of graphs is not suitable for quantitative interpretations. The reason is that the elongation rate of various kinds of cells differs at the same distance from the tip, since it depends on the length of cells at the beginning of the elongation zone.

#### SUMMARY

The aim of this work has been to bridge the gap between the researches on the course of cell elongation in the root, i.e. the approach followed by Burström, and on the distribution of growth in the root, i.e. the line of investigation represented by Goodwin and Erickson. For this purpose both the distribution of growth and the course of cell elongation have been determined on the same roots of wheat.

A new variant of the displacement rate method has been introduced for determining the distribution of growth. It is based on measurements of the length of cells in a file.

It has been found that the course of cell elongation reported by Burström (fig. 1), with the characteristic sudden retardation of elonga-

tion with time, corresponds on the whole to the distribution of growth reported by the representatives of the other line of approach to the problem, i.e. with growth characterised by a gradual decrease of the elongation rate in the basal part of the elongation zone.

The supposition advanced in an earlier paper, that the relative rate of elongation is constant throughout the cell division zone in the root, has been confirmed.

*Institute of Plant Anatomy and Cytology*  
*University of Wrocław*

(Entered: 15.4.1960)

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