A re-evaluation of the mechanism of root contraction in Monocotyledons using the example of *Arisarum vulgare* Targ.-Tozz. (*Araceae*)

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Summary

Within the Monocotyledons the anatomical ring-collapsing type of root contraction is very common. However, up to the present there has been no overall view of the anatomical changes and how they relate to the pulling and moving function of the root. The careful maceration of contractile roots of *Arisarum vulgare* makes it possible to measure the dimension of the cells, particularly the dimensional change during root contraction. It can be shown that the outer and middle cortical cells expand radially (increase in volume, growth) with simultaneous longitudinal shortening, and finally collapse. The inner cortical cells of *Arisarum* show a longitudinal shortening which is synchronous to that of the outer and middle cortical cells. The inner cortical cells retain their original volume, which means that no cell growth occurs.

Occasionally, expansion and shortening of the outer and middle cortical cells occur at different times. Then, first a radial expansion of the cells is seen, followed by their shortening.

A consideration of the early results shown in *Acidanthera* seem to make it possible to suggest a unified anatomical model of root contraction. In this model, radial expansion and longitudinal shortening are two processes of activity of the cortical cells which, in principle, take place separately in time and space. Both activities are important for underground plant movement. Contrary to all earlier models it is assumed that the inner cortical cells shorten actively and thus produce a pulling force acting on the innovation system of the plant. This shortening activity can be limited to the inner cells (e.g. *Acidanthera*), but it may be that it also takes place in the middle, and even in the outer cortex (*Arisarum*). However, the main activity of the middle and outer cortex is the radial expansion which has nothing immediately to do with root shortening!

Radial expansion develops a force which results in a sideward pushing of the soil (pushing force, work of expansion) and therefore makes movement in the soil easier (channel effect). The collapse of these cells promotes shortening passively.

Key words: Root contraction, contractile root, *Arisarum*, Monocotyledons

Introduction

Through the activity of contractile roots many plants are able to move in the soil. These movements are very slow, and, in most cases, only a few centimeters or millimeters per vegetation period (see e.g. Rimbauch 1895, 1897, 1897a, 1898, 1898a, 1902, Woodhead 1904, Galil 1962, 1969, 1980, Pütz 1991, 1993, 1994). This movement is possible because the roots contract actively and build up a considerable force (Pütz 1992, 1992a). The question as to how the root is able to produce this force has been the subject of a number of papers, attempting to describe the anatomical changes before and after the shortening process. The active mechanism of root contraction has been discussed with respect to interesting details and observations. However, up to now, a definitive clarification has not been produced. The next chapter (Summary of literature) will make clear that different anatomical patterns allow us to make a distinction between a storey-collapsing and a ring-collapsing type of root contraction. Moreover, within the ring type there are at least three interpretations as to how root shortening may occur. Thus, it is not surprising that up to now an overall view to the mechanism of root contraction in the Monocotyledons does not exist. One reason for the different interpretations within the ring type might be that several authors have not really considered the continuity of shortening. Moreover, a qualitative description of cell changes is not sufficient. Again, semiquantitative measurements in serial cuts are problematic. As we stated in
an earlier work (Pütz et al. 1990), it seems hardly possible to make wall-parallel cuts through cells, in particular through the inner cortical cells, which are very long but very thin (e. g. 680 × 25 μm; JÜRNESTEDT 1984). Non-parallel cuts result in cells being arbitrarily cut off and measured cell dimensions of dubious reliability. However, besides the anatomical analysis, the only other important basis for understanding root contraction is an exact, statistical determination of cell dimension, since this makes it possible to describe the continuous anatomical process. A reliable method is the maceration procedure shown by Pütz et al. (1990), which makes it possible to measure the cell dimension of just about every tissue sample of the root. Up to the present this method has been used with one species. Further investigations, which might reveal the existence of further mechanisms behind the ring type, are necessary. A good subject for examination seems to be *Arisarum vulgare*, which according to Galil (1978) shows a very special root anatomy. On the basis of the *Arisarum* results we will try to develop an overall concept as to how the ring-collapsing type of root contraction may work.

**Summary of literature**

Many papers deal with the anatomical mechanism of root contraction in Monocotyledons. Several possibilities seem to exist as to which anatomical changes appear in the root due to its shortening.

1. The storey-collapsing type

In their longitudinally cut contractile roots, a few Monocotyledons show a characteristic feature of layers of collapsed cortex cells arranged in storeys, together with a spirally undulated stele, erect before root contraction took place (see scheme in Fig. 1 A). This type can be found in the Tribus *Brodiaeeae* within the sub-family Allioideae (taxonomy according to Dahlgren et al. 1985), e. g. *Brodiaea lactea* (Smith 1930; THODAY 1931), *Dichelostemma spec.*, *Triteleia spec.* and perhaps in some orchid roots e. g. *Dactylorhiza* (Kirschner et al. 1936, p. 546) Smith (1930) describes the cortex cells as increasing in radial and tangential direction by a combination of growth and turgor, while simultaneously decreasing in length. These changes have not been verified quantita-

Fig. 1. Diagram of the different feature patterns of root contraction: A) storey-collapsing type. B) ring-collapsing type. Co = collapsing cells, Ce = cortical cells, Ex (arrow) = expansion, Cr = cryptocorm (e. g. bulb, corn), Sh = shrinkage, St = Stele.

2. The ring collapsing type

The contracted roots of most Monocotyledons show another pattern of features (compare diagram in Fig. 1 B). Most apparent is a ring of collapsed cells situated beneath the exodermis. Secondly, in most cases one can find radially expanded cortical cells, compare e. g. *Gravis* (1926) in *Circinum capense*; Proffer (1931) in *Gladolus*; Wilson & Honey (1966) in *Hyacinthus orientalis*; Lamant & Hellier (1967) in *Arum italicum*; Chen (1969) in *Narcissus pseudonarcissus*; Delore (1980) in *Allium polyanthum* and Jürenstedt (1984) in *Chlorogalum pomeridianum*.

It is generally believed that the macroscopic feature of contractile roots, the shrinkage of the root surface (Sh in Fig. 1) is a passive reaction to the shortening process within the root. Also, the tissues of the stele are compressed passively. This can be seen, e. g. by the turns of the spirals of metaxylem vessels being closer together or by the minute wavy folds of the longitudinal walls of individual cells (compare e. g. Wilson & Howey 1966, Chen 1969, Jürenstedt 1984). The root cortex is divided by many authors into several compartments, i. e. inner, middle and outer cortex, and can best be seen at a cross section of a root just before contraction (e. g. see Fig. 3 H). The cells of the root cortex seem to be responsible for the active shortening process. However, various opinions exist concerning (1) the exact localisation of the active layers and (2) which changes in cell dimension occur.
2a. Cells of the root cortex expand radially while shortening longitudinally. These changes were found by comparison of sections of contracted parts of the root with those of non-contracted parts. However, only a few papers present comprehensive measurements (e.g., Ruzin 1979, Delsore 1980, Jernstedt 1984). Localization of the active cells is obtained from the cross sections, where the radial expansion of the cortex cells seems to reflect their shortening activity. Some authors describe this activity as starting at the middle (maybe together with parts of the outer) cortical cells and afterwards spreads continuously to the inner cortex cells (Lamant and Heller 1967; Jernstedt 1984). After expansion the active cells collapse. Other authors describe the inner cortical cells as being active mainly in expansion and shortening, while the outer cells are collapsed (Wilson and Honey 1966; Chen 1969; Reynolds and Van der Schuyff 1974 in Eucampt; Deloret 1980). Wilson and Honey (1966) have done some ultrastructure examinations of the cell walls relating to the intracellular process resulting in an active expansion and shortening of the cell. They require a re-orientation of cell growth (from the normal longitudinal extension growth to a radial expansion). Special structural features of the cell wall should lead to an anisotropy of cell wall extensibility, so that cells automatically shorten during their radial expansion (Wilson and Anderson 1979, Jernstedt 1984a). Also, Chen (1969, in accordance with De Vries 1880) does not exclude a participation of turgor pressure in the first phase of shortening, leading to a shorter spherical shape of the isotropic cell.

2b. Church (1919, Cooperia drummondii) and Arber (1925, Hypoxis decumbens) cannot find such a shortening of the radially-expanded cells “... the case of Hypoxis has left me completely puzzled, for I cannot detect such shortening as that postulated ...” (Arber 1925, p. 21). Ruzin (1979) comes to a very similar result: “Middle cortical cells show an increase in width but length remains unchanged” and “Inner cortical cells do not increase in volume (i.e., no growth) but increase in width while shortening longitudinally”. His results lead Ruzin to describe a growth/collapse mechanism of root contraction (Ruzin 1979, Fig. 13 and the last three chapters of his discussion): “The orientation of the expanded diameter of the root contiguous with the non-expanded portion of the root distally produces a longitudinal tension along the axis of the root. Active shortening of individual cortical cells does not occur ...”. In Ruzin’s hypothesis, the outer cortex has an important function as buffer cells, because the successive collapse of these cells keep the longitudinal tension constant over a longer period. The inner cortex cells shorten comparably, which is necessary to equalize the longitudinal tension. Ruzin detects a partial dissolution of the middle lamellar material of the innermost cortex cells and therefore interprets their shortening as passive. Petz et al. (1980) have examined Acidanthera bicolor, another member of Tridaxae. Very similar features to those of Freesia were found, which seems to support the Ruzin mechanism.

2c. Common to the two interpretations described above (2a and 2b) is that a longitudinal tension is described, resulting in a pulling force ultimately producing an underground movement. Galili (1975b) takes the view that the contractile roots of Arisarum vulgare differ. The cortex cells of the roots of this species do not shorten longitudinally, but do so transversally. Galili describes a radial expansion of the cortical cells and afterwards a decrease in the same direction (collapse). According to Galili (1969) these “transversal-contractile pioneer root” do not show any longitudinal shortening and produce no pulling force. The function of these roots is to push away the substratum and to produce a space within the soil for the growing corn.

Materials and methods

Corms of Arisarum vulgare Targ.-Tiez. were collected in Cinque terre, Italy and on Paros, Greece and then cultivated in the greenhouse of the Botanical Institute of the K. W. T. H. Aachen (for details of the corm see Galili 1978). Plants were dug out several times during their vegetative period, and contractile roots were cut off and fixed in 1% E (FAA).

Activity of contractile roots is characterised by two features: proximal swelling, and shrinkage of the root surface. Therefore, according to Ruzin (1979) and Petz et al. (1980) different zones of the root can be distinguished:

Zone 0: distal part of the root which will never shorten
Zone 1: pre-contractile, part before swelling and shrinkage
Zone II: contractile, swollen part of the root
Zone III: post-contractile, shrinkage of the root surface

The zones blend into each other (see Fig. 2) with swelling and shrinkage continuously spreading out in the direction of the root tip, so that at a single point of the root we find first zone I, followed by zone II and finally by zone III. However, towards the root tip swelling becomes smaller, and, after a length of about 5–8 cm, no more swelling occurs.

The zones make it possible to distinguish various stages of root age (Fig. 2), where (A) is a root at the beginning of swelling activity, (B) is a root after swelling activity and (C) and (D) represent the corresponding transitional stages.

Cross section of 1 mm thickness (sample) were removed from the roots shown in Fig. 2 from locations distributed...
evenly over the roots (see the white lines in Fig. 2). Furthermore, two roots of each of the stages (B) and (C) were completely cut in cross sections of 1 mm thickness. All samples were preserved in AFE (FAD).

Maceration took place according to the description of Pätz et al. (1990). A sample was placed in 15 ml cold 0.5% KOH solution and boiled for 12 min. Under the binocular, cell groups from the inner, middle and outer cortex were isolated and rinsed with distilled water in a glass vessel 3810 (Eppendorf). (For exact localization of the cell groups see Fig. 3.) Shaking the vessels produces single cells in a suspension, from which 50 cells were measured with an ocular micrometer at a magnification of 60. The largest dimension of a single cell was taken to be its length.

Discussion of the method

Pätz et al. (1990) have verified the suitability of the maceration method in principle. A 2 mm thick sample of the expanded part of a root was taken. One half of the sample was macerated and cross and length cuts were made from the other half. The dimension of the outer cortex cells from the maceration were compared with the cell dimension measured from the cuts. A very high correlation was found and it was therefore concluded that the results of the maceration method could be taken to show the changes in cell dimension in contractile roots.

This verification has been carried out for Arisarum from a root part of zone III. The results are shown in Tab. 1, and allow some conclusions:

1. The difference between longitudinal and radial dimension is significant, in the maceration as well as in the cuts. It can thus be stated that our decision to take the largest dimension as the length seems to be right.
2. Expansion of the cortical cells occurs in the radial as well as in the tangential direction. The cuts in Tab. 1 show that radial expansion is even greater than tangential expansion. When measuring macerated cells it is impossible to distinguish between radial and tangential dimension, and thus it is clear that the tangential dimension has been measured as radial to some extent. As a consequence it can be seen in Tab. 1 that the radial dimension with maceration is smaller than with cuts. However, this error is minor since when comparing the different hypotheses the total dimension of length is required rather than the maximum radial expansion.

Results

The anatomical patterns

The anatomical changes during contraction of an Arisarum root are very similar to the ring collapsing type. The series of cross cuts in Fig. 3 makes clear the
Fig. 3. *Artemisia vulgaris*, cross cuts through different zones of a contractile root. The surrounded areas show cell portions analyzed as inner, middle or outer cortical cells. I – III = zones of activity, En = endodermis, Ex = exodermis, IC = inner cortex, MC = middle cortex, OC = outer cortex, Co = collapsed cells, BC = begin of collapse.

strong radial expansion of cortical cells from zone I to zone II. Since expansion occurs at centripetally situated cortical cells, the process of collapsing occurs at the expanded cells (BC in zone II/III). These collapsing cells divide the expanded cells into middle and outer cortical cells. Expansion and collapse continue, so that in old contractile roots most of the cortical cells in zone III are expanded and for the most part collapsed. This leads to a thick band of collapsing cells at the periphery of the root cut, as for example can be seen at the longitudinal cut in Fig. 4 III. Comparison of this cut with that of a non-contracted part (zone I, Fig. 4) again shows the expansion and collapsing process. Moreover, these cuts make clear that a detailed quantitative analysis of cell dimension seems to be problematical due to their apparently wide variability. However, it is important to mention that cell form is very similar in cuts and in the maceration. Finally, several authors (Wilson & Honey 1966, Chen 1969, Ruizin 1979) report a folding of the longitudinal cell walls, and interpret this to be passive. These folds are visible in *Artemisia* roots too, but are limited on the central

Fig. 4. *Artemisia vulgaris*, longitudinal cuts through contractile roots in zone I and zone III. En = endodermis, Ex = exodermis, IC = inner cortex, MC = middle cortex, Co = collapsed cells.
Results of maceration

The real changes of cortical cell dimension can be found in macerated cells, the averages being given in Fig. 5. Each of the roots, differing in their age, clearly shows a clear radial expansion (R) of the middle cortical cells. The inner cortical cells show no expansion.

Obvious changes also can be seen in cell length, which occurs simultaneously in all cortical cells, independent of cell expansion. Cells shorten approximately by half. Furthermore, the beginning of shortening of middle (outer) cortical cells starts at the same time as cell expansion occurs. This means that

\[ \text{in the roots (B), (C) and (D) the outer cortex was also measured. The cell dimensions were identical with those of the middle cortical cells, so that graphical illustration can be dispensed with in Fig. 5.} \]

\[ \text{a swollen root (zone II, samples (B) 1–3, (C) 3–4) is then actively shortening. Shortening also occurs in zone III, at which time the root surface is already transversely folded.} \]

\[ \text{For further accurate evidence as to when expansion and shortening occur, some roots of stage B (Fig. 6) and C (Fig. 7) were macerated completely. All showed that the shortening of the cortical cells occurs simultaneously, normally beginning in zone II. However, sometimes, as in root C, the process of shortening starts very late in zone II/III. In this root, expansion of middle and outer cortical cells for} \]

\[ \text{Comparison of the results within the sample series (e.g. set 2, set 3, see Fig. 2) show the same curves as in Fig. 5. This ensures that the proximal shortening process does not influence the dimension of distally-situated cells. The procedure of previous workers in describing the anatomical changes during contraction in one single root is possible in principle. However, it has to be mentioned that root activity decreases in the distal direction (Chen 1969, Rozhn, 1979). Thus, it has to be taken into account that the root part under examination would have become contractile.} \]
Fig. 6. *Arisum vulgare*, changes of dimension of the cortical cells in two roots of root age B during the contraction process. The abscissa represents the sample number (these roots have been completely cut into samples). For orientation the roots have been schematically drawn in the middle. Each point is the average of at least 50 single measurements, the dotted lines symbolize the standard deviation. L = longitudinal, R = radial.

Table 2. Cell dimension and volume of inner and middle cortical cells before and after root contraction. Each average is of 150 single measurements, all volumes in 10³μm.

<table>
<thead>
<tr>
<th></th>
<th>root C</th>
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<th>root C</th>
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<td>pre-</td>
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<td>pre-</td>
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<td>contractile</td>
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<td>618 ± 127</td>
<td>374 ± 139</td>
<td>inner</td>
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<tr>
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<td>middle</td>
<td>521 ± 100</td>
<td>313 ± 83</td>
<td>middle</td>
<td>561 ± 113</td>
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<tr>
<td>radial</td>
<td>inner</td>
<td>35 ± 7</td>
<td>47 ± 12</td>
<td>inner</td>
<td>33 ± 7</td>
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<tr>
<td></td>
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<td>66 ± 10</td>
<td>152 ± 23</td>
<td>middle</td>
<td>69 ± 11</td>
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<tr>
<td>tangential</td>
<td>inner</td>
<td>35 ± 7</td>
<td>47 ± 12</td>
<td>inner</td>
<td>33 ± 7</td>
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<tr>
<td></td>
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<td>91 ± 14</td>
<td>middle</td>
<td>69 ± 11</td>
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<tr>
<td>volume</td>
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<td>7.8 ± 3.6</td>
<td>8.5 ± 4.7</td>
<td>inner</td>
<td>7.3 ± 3.8</td>
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<tr>
<td></td>
<td>middle</td>
<td>22.7 ± 7.9</td>
<td>43.3 ± 14.1</td>
<td>middle</td>
<td>24.0 ± 9.3</td>
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a greater part has happened before shortening starts. The other roots show that expansion and shortening of the middle and outer cortical cells occurs simultaneously.

Calculation of cell volumina

Exact measurement of cell volumina with maceration is impossible, because the tangential dimension cannot be measured. The cross cut series (Fig. 3) makes clear that the radial and tangential dimensions of non-expanded cells are almost identical (compare Pütz et al. 1990), and it thus seems to be a useful approach to calculate the volume by multiplying the length with the square of the radial.

In the expanded cells the tangential expansion is smaller than the radial expansion. Measurements at cross cuts (Tab. 1) show that this reduction can be expressed by multiplication of the radial dimension with the factor 0.6. Thus, the volume of expanded cells can be calculated by multiplication of cell length, radial dimension, and radial dimension multiplicatated with 0.6. Such calculations were carried out as examples for some samples of root C. All single measurements of the samples 24, 23 and 22 (root C, Fig. 7), or 22, 21 and 20 respectively (root C1, Fig. 7), are cortex cells before contraction (precontractile), while samples 1, 2 and 3 are cells after shortening (postcontractile). First, the volume of each cell was calculated so that the average volume of cortex cells could be recorded with the standard deviation (Table 2).

These values show that the middle and outer cortical cells have a volume increase despite shortening, and that this increase can be as much as twofold. The volume increase of cortical cells in contractile roots has also been described by other authors, and was seen as cell growth (Wilson & Honey 1966; Wilson & Anderson 1979; Jeerstedt 1984). However, shortening of the inner cortical cells takes place at constant volume (see Tab. 2, compare Ruzin 1979, Pütz et al. 1990). This makes clear that the change of dimension in the inner cortical cells takes place without cell growth.

Fig. 7. Arisarum vulgare, changes of dimension of the cortical cells in two roots of root age C during the contraction process. The abscissa represents the sample number (this roots have been completely cut into samples). For orientation the roots are schematically drawn in the middle. Each point is the average of at least 50 single measurements, the dotted lines symbolise the standard deviation. L = longitudinal, R = radial.
Discussion

Gale (1978) describes the roots of *Arisarum* as ‘transversal contractile pioneer roots’, whose cells have no longitudinal shortening. Our maceration results now described show that this statement is untenable. Besides expansion, a longitudinal shortening of about 50% can be recognised.

Middle and outer cortical cells increase radially while shortening in length. These changes continue distally and centripetally, extending to most of the inner cortical cells. The various observations of the active cell layers in hypotyposis 2a (see Summary of literature) probably result from different times of observation (compare series in Fig. 3), whereas examination of roots of phase B or C (Fig. 2) shows outer and middle cortical cells expanding and shortening; examination of roots of D or E shows the outer and middle cortical cells collapsed with cell changes having occurred in the inner cells. This could be easily verified using some hand cuts of various old contractile roots (phase B, D, E) from *Narcissus tazetta* and *Hyacinthus orientalis* var. ‘Lady Derby’. It can thus be stated that the anatomical changes of *Arisarum vulgare* are very similar to those found in, e.g. *Narcissus* (Chen 1969), *Hyacinthus* (Wilson & Honey 1966, Wilson & Anderson 1979) or *Chlorogalum* (Jernstedt 1984), where cell growth, together with an anisotropy of cell wall extensibility, produces cell expansion with simultaneous shortening.

Our macerations show that shortening of all cortical cells occurs synchronously, a phenomenon which has not previously been taken into account. However, this synchronous shortening is necessary since active shortening of cells within a tissue is only possible if the adjacent, passive cells also shorten. As an important consequence of this synchronous shortening, the active component of shortening is not localized, and it may be that all cortical cells are active, or only some compartments, e.g. the inner or middle cortex. Previous researchers have attributed the active shortening to those cells which also shows active expansion. There may be justification for this connection between active shortening and active expansion, yet it is by no means indispensable.

Continuous quantitative analysis of *Arisarum* contractile roots makes clear that expansion and shortening of the middle cortical cells can occur at different times (root C in Fig. 7). This goes against the opinion that radial growth, together with anisotropy of cell wall extensibility, would produce simultaneous shortening.

The mechanistic approach of Ruzin

This problem, relating cell expansion to root contraction, is in principle the same for the growth/collapse mechanism of Ruzin (1979). He postulates, for *Freesia* contractile roots, a longitudinal tension directly created by the expansion of the middle cortical cells. These expanding cells do not shorten, but collapse (the same applies to *Acidanthera* contractile roots, Pütz et al. 1990). For direct comparison with the *Arisarum* results, the results for *Acidanthera bicolor* for a root of phase C are again shown in Fig. 8 (from Pütz et al. 1990: middle/outer cortical cells expand and collapse without noticeable shortening, while inner cortical cells in zone II show a marked longitudinal shortening without simultaneous radial expansion). These changes may be typical for *Iridaceae*. However, it is not yet clear how it is possible to create this very strong longitudinal tension by radial expansion. Expansion surely leads to tissue tension within the root, as, e.g. Burström (1971) has postulated for *Triticum* roots. He expects this tension in *Arum* contractile roots too (Lamant & Heller 1967). It may be that this tension increases considerably and produces a shortening of the proximal root parts. However, shortening would also affect the expanded cells. In the proximal root parts cells of *Acidanthera* or *Freesia* avoid this longitudinal tension by collapsing. We think that collapsing of the cells would provide enough space within the root for equalization of the tension in general, and shortening of the root would not occur. Strank (1991) has worked on root contraction to show some aspects in a mathematical quantitative model. His FEM calculation (finite elements) supports that radial expansion has only a very local effect in producing longitudinal tension. He concludes: “Es sind offensichtlich keine gro ß en Spannungen, die da in der Zone der aktiven Kontraktion nach oben und unten weitergeleitet werden”. Pütz et al. (1990) have also discussed the problem of tension transfer up to the cryptocorm. Another possibility for the transfer of axial tensions lies with “non-extensible elements”, stretched between crypto-

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4) As an alternative, dissolution of the cell wall and separation of the cells would lead to a decrease in the total length of the active root part, but without shortening of the passive cells and, therefore, of no consequence for the mechanism. It should be mentioned, that Sterling (1972) has discussed such a mechanism for *Gladiolus* (“interdigitation”). Wilson & Anderson (1979) and Ruzin (1979) have shown anatomically and physically that this postulate is untenable.

7) Expansion continues centripetally and will occur in the inner cortical cells, so that in older roots (D) these cells also expand (see Pütz et al. 1990, Fig. 5).
Possibility of a new unified model

In the search for anatomical conformity between *Arisarum* and *Acidanthera*, the diagram in Fig. 9 was prepared to make clear the dimension of the root cells within the different zones. There are two similarities: middle/outer cortical cells expand radially and inner cortical cells shorten. The main difference is that in *Arisarum* the middle/outer cortical cells also shorten. Rejection of the overall view that sees expansion and shortening in a single context makes it possible to postulate that the inner cortical cells shorten actively. We therefore suggest a new overall anatomical mechanism of root contraction, in which two different processes of activity can be distinguished (see the arrows in Fig. 9)

(1) active shortening of the inner cortical cells
(2) active radial expansion of the outer and middle cortical cells

Effects of shortening of the inner cortical cells

Shortening tension directly affects the inner root parts (e.g. the stele), which will be passively compressed. Familiar features are, e.g. the turns of the spiral of metaxylem vessels being situated closer together, or the folds of longitudinal walls (compare e.g. Wilson & Honey 1966, Chen 1969, Ruzin 1979). Another possibility is a spiral winding up of individual xylem vessels (e.g. *Tigradia pumonia*, *Xanthorrhoea preissii*).
Cells of the middle and outer cortex passively respond to the shortening process on the one hand by collapsing (e.g. Actinodaphna). On the other hand, if the process of collapsing is slowed down, the cells shorten passively (e.g. Antirrhinum, see Fig. 7). Localization of shortening activity to the inner cortical cells still has to be investigated. It may be that the active part extends to middle or even outer cortical cells in some species. One examination method could be the observation of cells in vivo within their tissue, so that change in dimension could be localized directly. At present we are trying to develop such a method.

Effect of radial expansion of middle and outer cortical cells

The function of active shortening is to produce a pulling force to move a corolla or a bulb against soil resistance. The radial expansion of middle and outer cortical cells has nothing to do with the pulling force. Cell expansion leads to a swelling of the root, which probably has another important function during plant movement by contractile roots. Through swelling the root pushes the substratum to the side, and after collapse a soil cavity results. This cavity reduces soil resistance and therefore makes plant movement in the soil easier. Taking this into account, the description of very thick roots as "pioneer roots" (Galil 1969, 1978) is acceptable. This soil pushing is not only to be found with specialists (e.g. Oxalis, Galil 1968, Pütz 1994) but is a general aspect of contractile roots (channel effect, Pütz 1992).

Outlook

Our model takes account of the anatomical features and changes with respect to the function of contractile roots as moving organs. Most previous researchers have neglected this. There are two forces created by a contractile root: the pulling force due to active cell shortening and the pushing force due to radial expansion. Experimental simulations make clear that the pushing force in some cases leads to a very high energy advantage (Pütz et al., in press).

The conspicuous cell expansion has diverted attention from the actual localization of active shortening. However, our present hypothesis makes it possible to redraw the various observations within the ring contractile type to a single mechanism of root contraction. In this way, further investigation can focus on some important points still outstanding, it being necessary to obtain more information about active shortening of the inner cortical cells.

On the other hand, by postulating an active shortening of the inner cortical cells, one main aspect of root contraction can be seen in a new light. To answer the question as to how the active shortening occurs intracellularly one has to take into consideration that shortening occurs at constant volume. Strank (1991) shows several possibilities, functioning when no cell growth takes place. Earlier investigations into the position and orientation of fibrils and microtubuli in cortical cell walls of contractile roots (Lin & Jerne'stedt 1988, Cvr et al. 1988, Smith-Huerta & Jerne'stedt 1989, 1990) were based on the belief that there is a growing process of the cell. Observations fail to make clear whether the fibri changes during contraction are part of an active process or a passive reaction to equalize an axial tension, and therefore maybe cannot produce a satisfactory explanation of the intracellular mechanism of root contraction.

Chen (1969, in accordance with De Vries 1880) does not exclude a participation of turgor pressure in the first phase of contraction, leading to a spherical shape of the isotropic cell, i.e. a shortening without any growth. Strank (1991) has done some preliminary examinations of in vivo maceration and found a tendency of the cortical cells of Lapeirousia and Watsonia contractile roots to round up. Unfortunately, he did not localize inner, middle or outer cortical cells. Thorous in vivo maceration experiments might provide important information about the contraction mechanism. In this context it would be necessary to calculate if this "cellular rounding up" can reach a cell shortening of 30%.

In recent years there have been some investigations of moving processes produced by the activity of actin. Thus, e.g. Menzel & Elsner-Menzel (1989) describe an actin-based cytoplasmic contraction in Acetabularia. It may be helpful to investigate whether the inner cortical cells of contractile roots would shorten in this way.

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Buchbesprechung


So spiegelt sich in Begriffen wie Modul, Phalanx-Wuchsform oder Mosaik-Zyklus die wachsende Bedeutung von bestehenden Teildisziplinen wie Populationsökologie und Ökosystemforschung wider.

Anzuerkennen ist das Benehmen um eine präzise Definition. Dies hat dort seine Grenzen, wo unterschiedliche Interpretationen möglich sind oder regionale Bedeutungsunterschiede zum Ausdruck kommen.


Zu begrüßen ist, daß das englisch-deutsche Register sowie die Einfügung englischer Übersetzungen für die Mehrzahl der verwendeten Begriffe weiter ausgebaut wurde. Dabei bleibt manchmal unklar, warum der Autor die englischen Termini nicht konsequent ins Deutsche übertrug, so z. B. steht für importance value – importance value, für ingestion – Ingestion.

Die Neuausgabe der „Ökologie“ in der Reihe der Wörterbücher der Biologie wird wie die vorangegangenen Auflagen ein breites Interesse bei allen denen finden, die an einer ausgewogenen, umfassenden Sammlung und Verbreitung ökologischer Stichwörter und Begriffe interessiert sind.

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