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In vivo tissue isolation in contractile roots of *Lapeirousia laxa* (Iridaceae)

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Summary

The *in vivo* tissue isolation technique presented here allows localization of tissue tension within contractile roots, and thus, localization of a potential to shorten. Tissue strips of the stele, inner cortex, and outer root parts no longer have shortening potential after isolation. However, defined tissue strips of middle cortical cells shorten immediately after isolation by 10–30%. This starts when root swelling appears (zone II/I), and continues up to root zone (III). The ability to contract seems to be limited to the expanded cells, which finally collapse. Thus, changes in the longitudinal cell dimension of these expanded cells does not occur in fixed roots. However, pressure to shorten affects the inner and outer root tissues, which shorten passively. Innermost cell layers of the root cortex show partial dissolution of middle lamellar material, and thus, cell wall bubbles appear. In older roots (after contraction), cells of the inner cortex often become disconnected from each other and the inner cortex separates from the outer root parts. Quantitative comparison of cells before and after root contraction shows that the inner cortical cells become shorter by half.

On the basis of 'shortening potential', an alternative model of the mechanism of root contraction is presented. In this 'pneu-model', the active, middle cortical cells function like expanded 'elastic bands', and a small drop in cell pressure causes the expanded cell walls to lose their elastic tension, resulting in them shortening. This shortening creates a pulling force, which eventually effects underground movement.

Key words: mechanism of root contraction, *Lapeirousia laxa*, contractile root, tissue tension, pneu

Introduction

The common hypothesis of the anatomical mechanism of root contraction goes back to the studies of DEVRIES (1880), who found the cortex cells of contractile roots to be active. DEVRIES examined different tissue tensions within the root and found changes of dimension in cells lying in water (see DEVRIES 1880, Fig. 5 for *Cyanara scolymus*). The core of his study was: „Das Parenchym, sowohl des Holzkörpers als der Rinde, bildet den Sitz der Kontraktion, diese findet durch Wasseraufnahme statt, indem die Parenchymzellen sich verbreitern und verkürzen, dabei erhöhen sie ihren Turgor" (DEVRIES 1880, p. 77. Translation: Parenchyma from both the woody parts and the inner bark forms the seat of contraction, which is achieved by water uptake. Parenchyma cells expand radially and shorten longitudinally, thereby increasing turgor pressure.).

Furthermore, DEVRIES (1880) made a distinction between the immediate contraction in his experiments, and a gradual contraction in normally growing roots (originally cited in the text of DEVRIES (1880, p. 77) „allmälige Kontraktion der im Freien wachsenden Wurzeln"). The latter he interpreted as a growing process. RIMBACH (1898, 1929) found in his ink-mark examinations that many species show contraction of their proximal parts of up to approx. 70%. In contrasts to this, cell shortening in the experiments of DEVries (1880) was only approx. 1%.

However, especially in many monocotyledonous species, radial expansion of root cortical cells is very obvious. Thus, the experiments of DEVRIES (1880) are still the basis for interpretation of the anatomical mechanism of root contraction. It is interpreted to be a re-orientated cell growth: active radial expansion of cortical cells is linked with concurrent longitudinal shortening (WILSON & HONEY 1966; CHEN 1969; WILSON & ANDERSON 1979, DELOIRE 1980, JERNSTEDT 1984). The present paper deals only with the ring collapsing type of root contraction. However, anatomical behaviour in

contractile roots differs between species, and still unknown in many details. A short summary of literature is given in PÜTZ & FROEBE (1995).

Careful maceration of contractile roots of *Arisarum vulgare* (PÜTZ & FROEBE 1995) has made it possible to measure the dimensional changes during root contraction. Shortening and radial expansion of cortical cells occur at different times. Furthermore, inner cortical cells show a longitudinal shortening of approx. 50% without radial expansion, and it is useful to discuss the active role of these non-expanding cells in the shortening process of the whole root. In some species, shortening of the radial expanding cells has not been detected (ARBER 1925 for *Hypoxis*, RUZIN 1979 for *Freesia*, PÜTZ et al. 1990 for *Acidanthera*). In these cases, the mechanism of root contraction becomes completely incomprehensible. Therefore, RUZIN (1979) presented his 'growth-collapse mechanism', and postulated the shortening tension in the root being created by radial expansion of the cortical cells. Against this, PÜTZ & FROEBE (1995) postulated a direct, active role of the inner cortical cells as being responsible for root contraction.

Currently, our knowledge on root contraction is incomplete. Several hypotheses exist and appear justified, but a great step forward is only possible if we can localize a shortening potential directly in the root.

Materials and methods

Corms of *Lapeirousia laxa* (Thunb.) N.E.Br. were grown from seeds in the greenhouse of the Botanical Institute of the R.W.T.H. Aachen. During the first vegetation period (5 months), the plants were fully undisturbed in becoming healthy, adult corms of approx. 10 mm in diameter. After a resting phase of two months, the adult corms were cultivated in planting containers (5 litres), filled with riddled sand/loam mixture. Next, planting was carried out at regular intervals: every week, 10 containers were planted with 10 individuals each. 8–10 weeks after sprouting, roots were harvested, with 4-6 'suitable' roots in each container. 'Suitable' roots showed a clear thickening zone of a least 5 mm (zone II in Fig. 1). These roots were directly used in subsequent experiments. Some of the roots were fixed in AFE solution (mixture of 90 ml 70% ethanol, 5 ml 40% formalin and 5 ml acetic acid, according to GERLACH 1984).

To understand the anatomical changes during root contraction, hand sections (cross and longitudinal sections) were made from both fresh and fixed roots. Sections were stained with haematoxylin according to Delafied (GERLACH 1984). Cell drawings were made with the help of drawing device (Leitz, Wetzlar, Germany). In the longitudinal sections through different root zones (see Fig. 1), the dimensions of 50 cells in each of different parts of the root cortex were measured with an ocular micrometer at a magnification of 60 (localization of these cells in the root is shown in Fig. 4).

For *in vivo* tissue isolation, fresh contractile roots were divided into regions of a defined length of 5 mm (compare Fig. 1, Fig. 5). This was done using a special sectioning block, with two razor blades fixed together at a distance of 5 mm. Root portions were isolated from the root zones (III, II, II/I or I, see Fig. 1 in results). During the short time until tissue isolation (maximum 30 minutes), the 5 mm portions were placed in small Petri dishes filled with Gamborg solution (Gamborg B5, Sigma, Deisenhoven, Germany). For preparation of *in vivo* tissue isolation, two tangential, longitudinal section were made through a 5 mm root portion to obtain a 'middle root slice' of approx. 1 mm in thickness. This 'middle root slice' includes all tissues of the contractile root (exodermis, cortex, stele, see Fig. 1, 5 and description in 'Results'). The 'root slice' was placed into one drop of Gamborg on a slide, and was longitudinally sectioned in small tissue strips (for classification of these strips to contractile root anatomy see 'Results' and Fig. 5). Two minutes after isolation, the lengths of the tissue strips were measured.

In preliminary experiments, we examined the behaviour of similar tissue strips for two weeks to exclude further shortening. However, we did not find any shortening in addition to that taking place immediately after isolation.

Results

The most visible features of root contraction are shrinkage of root surface and root swelling (Fig. 1 A). It is thus useful to distinguish between different zones (according to RUZIN 1979, PÜTZ et al. 1990, PÜTZ & FROEBE 1995, see Fig. 1 B):

zone III: post-contractile, shrinkage of the root surface
zone II: contractile, swollen part of the root
zone II/I: starting zone: swelling of root occurs
zone 1: pre-contractile, root part before swelling and shrinkage

These zones blend into each other, with swelling and shrinkage continuously spreading out in the direction of the root tip. However, activity decreases, and after a length of approx. 5–7 cm, no further shrinkage occurs. This pulling activity occurs over a timespan of 30–40 days.

The anatomical features in *Lapeirousia* contractile roots are typical for Iridaceae contractile roots, and thus similar to the descriptions of, e.g., *Freesia* (RUZIN 1979) or *Acidanthera bicolor* (PÜTZ et al. 1990). The root cortex can be differentiated into outer, middle and inner cortex (Fig. 1 C, Fig. 2, 3). Most conspicuous is the middle cortex, which possesses 2–3 non-expanded cell layers lying centripetally at the boundary to the inner cortex. However, most of the middle cortex cells (approx. 10–12 cell layers, in large roots up to 20) show radial expansion during root contraction. Expansion begins in zone II/I (see Fig. 1 C, Fig. 2) and continues in zone II and zone III (Fig. 2). In the upper part of zone II

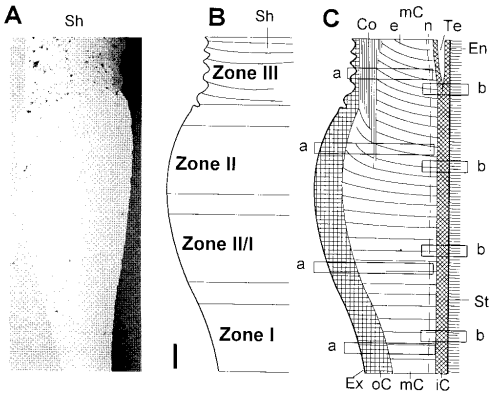

Fig. 1. Contractile root of *Lapeirousia laxa*. A. External shape. B. Drawing of root zones I–III = zones of activity, Sh = shrinkage. C. Schematic drawing of contractile root tissues. Rectangles 'a' show positions of cell drawings in Fig. 2, while rectangles 'b' represent drawings of Fig. 3. Co = collapsed cells, En = endodermis, Ex = exodermis, iC = inner cortex, mC = middle cortex (e = expanded cells, n = not-expanded cells), oC = outer cortex, Te = tearing of inner cortex. Bar represent 2 mm.

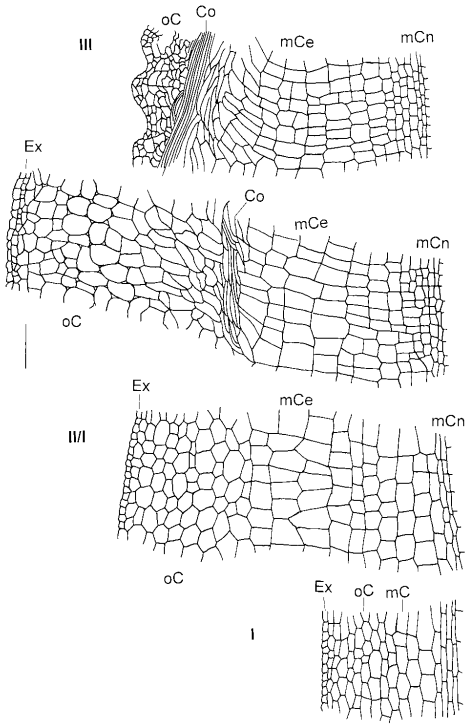

Fig. 2. Longitudinal sections through different zones of a contractile root of *Lapeirousia laxa* in the 'outer parts' (for exact position of sections compare rectangles 'a' in Fig. 1C). Bar represents 100 µm. Co = collapsed cells, Ex = exodermis, mC = middle cortex (e = expanded cells, n = not-expanded cells), oC = outer cortex.

(see Fig. 1C), the totally expanded cells begin to collapse (Fig. 2, zone II). This collapse starts at the boundary to the outer cortex.

The outer cortical cells (approx. 10 cell layers) show no expansion (see Fig. 1, Fig. 2). However, at the end of zone II, the outer cortical cells begin to collapse, and are totally collapsed in zone III (Fig. 2). This passive character of the outer cortex cells, and the pulling activity of the middle cortex cells, becomes obvious by examining the grouping of cells. In zone II/I in Fig. 2 cell rows are linear, whereas in zone II (Fig. 2) these rows are slightly curved, with the active parts of the middle cortical cells and the passive, outer parts being passively moved. This curvature of cell rows can also be seen in zone III (Fig. 2).

The inner cortex is located next to the stele and possesses 7–8 cell layers (see Fig. 3). At higher magnification, these cells are anatomically very apparent. In all zones, the cell walls are split (compare photographs in RUZIN 1979). Middle lamellar material between neighbouring cells breaks down in places, and thus, neighbouring cells appears as if they were 'stapled' together, with cell wall 'bubbles' appearing (compare WILSON & ANDERSON 1979, STERLING 1972). However, dissolution of the middle lamella seems to increase in inner cortex cells when examining zone II (Fig. 3). Here, cell wall 'bubbles' are much larger. Finally, in zone III, the connection between cells may disappear, and in most cases the inner cortex separates from the outer cortex and the exodermis (see Fig. 3, zone III, and schematically in Fig. 1C). Sometimes it can be observed that cells of the inner cortex may 'interdigitate' (compare STERLING 1972 for *Gladiolus*). However, in every case, the stele becomes disconnected from the outer root part in zone III.

RUZIN (1979) described shortening of these inner cortical cells in an 'accordion-like manner'. Comparison of the lengths of cells situated next to the stele in Fig. 3 (zone I) to Fig. 3 (zone III) also suggests cell shortening. In particular, measurements using an ocular micrometer (Table 1) demonstrate that the middle cortical cells expand radially to double their size without longitudinal shortening. On the other hand, inner cortical cells shorten longitudinally to half the length without

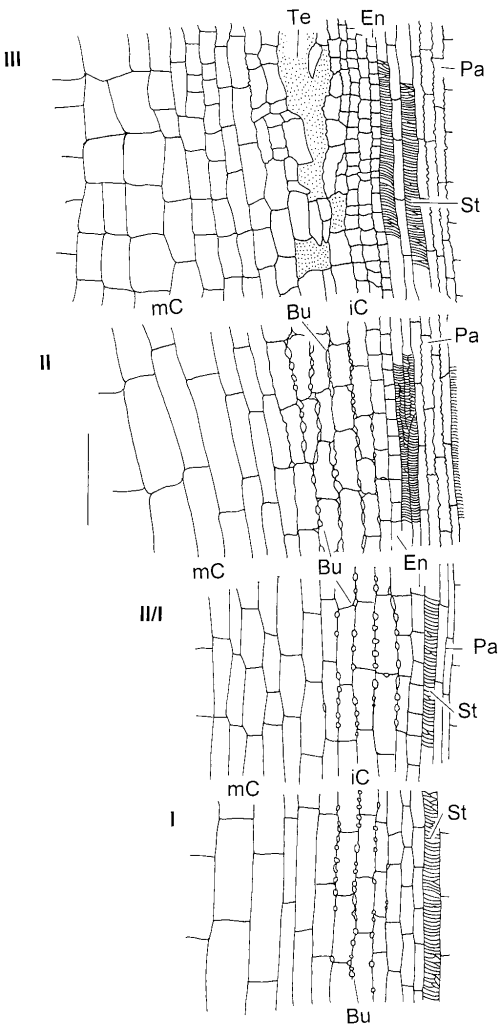

Fig. 3. Longitudinal sections through different zones of a contractile root of *Lapeirousia laxa* in the 'inner parts' (for exact position of sections compare rectangles 'b' in Fig. 1C). Bar represents 100 µm. En = endodermis, iC = inner cortex, mC = middle cortex, Bu = cell wall bubbles, Pa = parenchyma of stele, St = stele, Te = tearing of inner cortex (dotted).

radial expansion (for illustration see Fig. 4). These overall dimensional changes have been found in several Iridaceae species (RUZIN 1979 for *Freesia hybrida*; PÜTZ et al. 1990, for *Acidanthera bicolor*; PÜTZ unpublished

Table 1. Cell dimension (in µm) of cortical cells in different zones of a contractile root of *Lapeirousia laxa* (average of 50 single cells).

	inner Cortex		middle Cortex	
	longitudinal	radial	longitudinal	radial
zone III	86,6 ± 24,6	27,7 ± 3,7	39,9 ± 5,3	53,8 ± 9,4
Zone II	126,5 ± 22,1	29,2 ± 3,9	41,9 ± 6,8	57,8 ± 7,1
zone I	169,7 ± 34,7	26,3 ± 4,9	42,1 ± 4,0	29,1 ± 5,0

for *Tigridia pavonia, Crocus sativa, Gladiolus hybrid*), and thus might be typical for this family.

The tissue strips we isolated by *in vivo* tissue isolation are in most cases not at the anatomical tissue boundaries as described above (Fig. 1C). The various tissue strips (compare Fig. 5) include:

X = inner root parts: stele and inner cortex
C1 = middle cortex (centripetal part of middle cortex)
C2 = middle cortex (in zone I with part of outer cortex)
C3 = outer cortex, and, in most cases, centrifugal part of middle cortex
P = periphery root parts: exodermis and some layers of outer cortex

The values measured for dimensional changes to these strips in a single root are given in Fig. 5. In zone I, no modifications occur. In zone II/I, strips C1 and C2 shorten to 88% and 90% respectively immediately after isolation, whereas strip C3 only shortens to 95%. In zone II, this shortening process increases to a minimum of 76% in strip C1. Finally, in zone III, shortening to

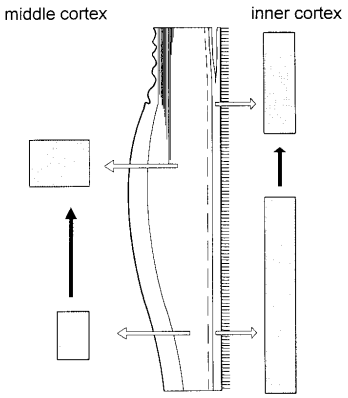

Fig. 4. Schematic introduction to the change in dimension of inner and middle cortical cells during root contraction. Middle cortical cells expand radially without longitudinal change. Inner cortical cells shorten longitudinally, but do not expand radially.

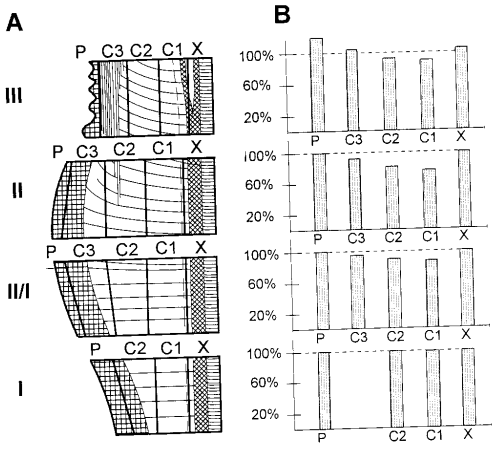

Fig. 5. *In vivo* tissue isolation of a single contractile root of *Lapeirousia laxa*. A. Position of tissue strips in the different root zones. B. Change in dimension of the tissue strips of a single contractile root immediately after isolation.

only 90% in strip C1. In contrast, the other strips increase in length, especially strip P by 20% and the inner root parts (strip X) by 10%.

These tissue tensions can be generally found in *Lapeirousia laxa* (Table 2). In every root measured shortening potential starts in zone II/I in the middle cortex (strip C1, C2). The maximum shortening potential of strips C1 and C2 is reached in zone II (maximum shortening of a single strip C1 measured was 67%).

Strip C3 in zone II/I and zone II shows an ability to contract only in the presence of middle cortical cells. In some roots, we were able to obtain C3 strips only from outer cortical cells, and these strips have no shortening potential (measurements of 14 roots). Inner and outer root parts became shortened passively. Thus, these strips extend after isolation. The maximum extending effect is found in zone III (in single cases, strip P extended by more than 50%, and strip X by 40%).

Table 2. Change in longitudinal dimension of *in vivo* tissue strips immediately after isolation (100% = 5 mm). Each average value is from at least 100 single measurements.

	P	C3	C2	C1	X
zone III	119 ± 13	103 ± 8	96 ± 8	91 ± 5	106 ± 8
zone II	101 ± 4	95 ± 5	89 ± 7	84 ± 5	103 ± 5
zone II/I	100 ± 0	96 ± 4	95 ± 5	92 ± 4	100 ± 0
zone I	100 ± 0	100 ± 0	100 ± 1	100 ± 1	100 ± 0

Discussion

Methodical annotation

The *in vivo* tissue isolation presented here is a simple technique, similar to the experiments carried out by DEVRIES (1880), who found tissue tensions and active shortening of cells to a magnitude of 1%. However, DEVRIES (1880) knew that root contraction is much higher, and thus he discussed the gradual contraction of the growing process. Exploration of a rapid and pronounced shortening effect (up to 33%) described here in *Lapeirousia laxa* contractile roots, is in opposition to this gradual contraction hypothesis. The main difference between the DEVRIES experiments and ours relates to the time of measurement. Active shortening potential of the middle cortical tissue is pronounced and occurs immediately after isolation. Thus, it is necessary to measure root (portion) length *before* tissue isolation. No previous investigators, including ourselves during a number of years, have taken account of this fact. We also carried out some preliminary experiments with turnips from *Mirabilis jalapa* (Nyctaginaceae), and contractile roots of *Narcissus tazetta* (Amaryllidaceae), *Arisarum vulgare* (Araceae), and *Galtonia candicans* (Hyacinthaceae) to test the importance of the time of measurement. In each case, we found isolated tissue shortening to the order of 15–30% immediately after isolation. The results of *Mirabilis jalapa* (Nyctaginaceae) will be presented in detail together with the anatomical contraction behaviour of this dicotyledonous plant.

Mechanism of root contraction

Active shortening of *in vivo* isolated tissues in *Lapeirousa laxa* contractile roots is a most important pointer in the discussion of the mechanism of root contraction. This shortening potential can be localized in the middle cortical cells. C3 strips showed no shortening potential, and therefore outer cortical cells are passive. Furthermore, 'grouping of cells' and the curved cell lines seem to confirm the passive character of the outer cortex.

We found no active shortening of inner cortical cells. These cells were part of strip X, together with the stele. Although we isolated the inner cortex from the stele within the strips X, in no case did we find shortening. Thus, inner cortical cells shorten passively, and typical features of passive cell shortening are, for example, wall folding (shown e.g., by WILSON & HONEY 1966, CHEN 1969, ZAMSKI et al. 1983), wall buckling (shown by RUZIN 1979, WILSON & ANDERSON 1979, PÜTZ et al. 1990), or, lastly, 'interdigitation' (shown by STERLING 1972). PÜTZ & FROEBE (1995) measured this cell shortening quantitatively in AFE-fixed contractile roots, and discussed its active role. However, the results presented

here make clear that the postulate of 'active shortening of inner cortical cells' is incorrect. In *Lapeirousia laxa*, we found that cell wall 'bubbles' became larger, and finally in zone III, cells separate from each other, and the inner cortex tissue becomes separated from the outer root parts. At this stage, the outer root tissues become lost, and the corm and distal root parts were only connected by the stele.

During initial root contraction, the stele is passively shortened. This can be seen from the turns of the spirals of the vessels becoming closer to each other (e.g. WILSON & HONEY 1966, CHEN 1969). However, continuous pulling effected by distal root parts (zone II) has to be transferred to the corm (which is to be pulled down). Thus, as PÜTZ et al. (1990) have pointed out, this passive stele shortening has to be fixed, for example, by apposition of cell wall material into the wall folds (WILSON & ANDERSON 1979, ZAMSKI et al. 1983).

In his growth/collapse mechanism, RUZIN (1979) postulated a longitudinal tension, produced indirectly by the radially growing cells. However, his postulation of an indirect tension effect is superfluous. Radially expanded, middle cortical cells shorten immediately and to a large degree if isolated from the other tissues. This means that middle cortical cells have a 'shortening potential', and are held in tension by the passive neighbouring tissues.

The remaining interpretation would seem to be cell growth mechanism (e.g., WILSON & HONEY 1966, WILSON & ANDERSON 1979, DELOIRE 1980, JERNSTEDT 1984): cells expand radially while shortening longitudinally. As indicated, this hypothesis is based on the examinations of DEVRIES (1880), and includes his view of a gradual shortening in the growing root. Indeed, the growing process of these cells is obvious in relation to their radial expansion (see Fig. 2). However, in Iridaceae contractile roots *(Lapeirousia laxa, Acidanthera bicolor, Freesia hybrida)*, shortening of the expanding cells cannot be found by anatomical examination, even if we compare cells of zone I with cells of zone III (see Fig. 4). The present study demonstrates that root contraction is due to the rapid-shortening potential of expanded cortical cells. However, up to the present, even precise investigation into the position and orientation of fibrils and microtubuli in cortical cell walls (LIN & JERNSTEDT 1988, CYR et al. 1988, SMITH-HUERTA & JERNSTEDT 1989, 1990), has not been able to make clear how 'active shortening' during radial growth is regulated at a molecular level.

Biomechanical model: the pneu model

KAPLAN (1992) discussed the mechanism of root contraction from a theoretical point of view. He criticised the overall „cellular" view, and demanded a view focusing more on the whole organism and its function. Understanding of the function of a contractile root requires us to consider its role as a moving organ. This moving organ produces a very strong force (compare PÜTZ 1996), which has an effect on, for example, bulbs or corms. In this 'constructional' context (compare PÜTZ & SCHMIDT 1999), we would like to present a biomechanical model. We propose calling this model of root contraction the 'pneu model'. The term 'pneu' is used according to OTTO (1976, p. 23): „The pneu is a system in which a layer stressed only in tension envelopes a medium." SCHILL (1976) presented a number of examples of botanical pneus, and BEREITER-HAHN (1976) discussed the role of the plant cell as a 'pneu'. In the context of contractile roots, the term 'pneu' seems useful because it indicates the mechanical function of contractile root in building up a pulling force for underground movement. Furthermore, 'pneu' covers both the organ 'root' and the division 'cell'.

The 'pneu' model of root contraction comprises two phases. During the first phase, longitudinal elastic stress is built up within the root. As a result of the present findings, we now know that this elastic stress is an active process by the expanding middle cortical cells, and begins in zone II/I. During this phase, considerable pulling tension is built up by the root. On a cellular level, we postulate that the middle cortical cell walls react like 'elastic bands'. During radial expansion of these middle cortical cells, the longitudinal walls become elastically expanded (compare WILSON & ANDERSON 1979, DELOIRE 1980), and thus store the energy for root contraction and pulling. However, there are no biomechanical data concerning cell wall elasticity in contractile roots.

In the second phase of root contraction, a (small) decrease of turgor pressure seems necessary. Remembering that the expanded cells lose their turgor pressure and collapse during root zone II (see Fig. 2), a drop in turgor – after expansion and before collapsing – seems possible. There are currently no physiological data in relation to changes of turgor pressure of the active cells. However, a drop in pressure makes the longitudinal expanded cell walls reduce elastic tension by active shortening (CHEN 1969, STRANK 1991). One consequence is an overall shortening pressure effect on the inner and outer root tissues to shorten passively, and indeed, a pulling force acting on the corm.

The 'pneu model' of root contraction has been conceived as an alternative to the common 'cell growth model'. It is important that all features, anatomical behaviour, maceration results, and tissue isolation are complementary, i.e. point in the same direction. Furthermore, the 'pneu model' makes it possible to explain the mechanism of root contraction in relation to its pulling function.

Outlook

A great deal of further investigation needs to be done. Firstly, further work should investigate whether 'active shortening' is a general feature in contractile roots, especially in species with other anatomical features, e.g. the storey-collapsing type in *Triteleia hyacinthina* (SMITH 1930) and *Oxalis incarnata* (THODAY & DAVEY 1932), or the hypothesis of 'bending resin vessels by expanding cells' in Apiaceae-roots (BERKEMEYER 1928).

Secondly, further work should be carried out at the 'cellular' level. At present, we know little about the levels of tissue pressure, elasticity of middle cortex cell walls, changes of turgor pressure in the active cells, and the control of cell expansion in contractile roots (see, for example, PRITCHARD 1994, EDELMANN & KUTSCHERA 1993, EDELMANN & KÖHLER 1995). Even a description of the 'elastic' cell walls in comparison to non-elastic walls remains to be produced.

Finally, SACHS (1873) demonstrated a shortening of roots just behind their growing zone in the order of 5–10%, which seems to occur generally in roots: „..., so daß ihr Turgor sich mindert, also Verkürzung durch elastische Zusammenziehung der betreffenden Zellhäute eintritt, ..." (Translation: „... thus, turgor pressure decreases, and shortening happens by elastically contraction of the cell walls ..."). Unfortunately, accurate investigation has not yet been carried out. We are left asking whether the shortening of contractile roots is merely an extreme increase in general root ability.

Finally, active shortening of middle cortical cells due to changes in turgor pressure and cell wall extensibility links the phenomenon of root contraction to other plant movements. A prominent example of plant movement is the mechanism of trap closure of *Dionaea muscipula* (HODICK & SIEVERS 1989), where cell wall extensibility and turgor play an important role. Another example comparable to root contraction is stamen contraction during pollination. In *Centaurea* spec., BÜNNING (1959) found 'contractile cells' shortening by approx. 10–20%. In *Berberis* spec., COLLA (1937) reported a shortening of up to 58%. The main difference between these movements exists in relation to induction and release of movement. Stamen contraction occurs rapidly and is a sensitive reaction on the stamen being touched. In contrast, in root contraction, formation of pulling organs is induced by external parameters (HALEVY 1986, PÜTZ 1997), the process of contraction being endogenous.

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