

Development and Function of Contractile Roots

Norbert Pütz

Institut für Biologie I, Rheinisch-Westfälische Technische Hochschule Aachen, Aachen, Germany

I. INTRODUCTION

Contractile roots are widespread among many plant species (Rimbach, 1926a, 1926b, 1927, 1929). They are very common in various families of the monocotyledons, for example, the Asphodelaceae, Hyacinthaceae, Alliaceae, Liliaceae, Amaryllidaceae, Orchidaceae, Zingiberaceae, and Araceae (families according to Dahlgren et al., 1985) but not, as far as is known, in the Poaceae and Cyperaceae. Root contraction is also present in several families of the dicotyledons; for example, Apiaceae, Fabaceae, and Oxalidaceae. Thus, it becomes clear that root contraction is not only specific to geophytes, but seems to be present in many life forms of plants (Raunkiaer, 1934) (we have encountered it in the seedlings of australian black boy [*Xanthorrhoea preissii*] as well as in tree seedlings [*Robinia pseudoacacia*]).

The typical feature of contractile roots is the shrinkage of the root surface at its proximal end. However, in most cases, another feature of contractile roots can be identified, because most of them swell in diameter before shrinkage. Thus, contractile roots show different zones during development. This can be seen in *Acidanthera bicolor* in Fig. 1:

- Zone I: precontractile zone, root before swelling and shrinkage
- Zone II: contractile zone, proximal part of the root is swollen
- Zone III: postcontractile zone, the surface of the proximal root part is wrinkled.

The zones blend into each other with swelling and shrinkage continuously spreading out in the direction of the root tip. Thus, at a single point of the root, we find zone I, followed by zone II, and finally by zone III. Normally, swelling is reduced toward the root tip, and at the end it is nonexistent. The contractile part of a root varies from species to species, but in general, it is approximately 4–10 cm long. Such zones make it possible to distinguish between various stages of root ages; that is, between a swollen active root (A in Fig. 1) and a root after pulling activity (B in Fig. 1). The root diameter in Fig. 1 changes from approximately 14 mm (A) to 7 mm (B). One very old contractile root even had a diameter of only 2–3 mm. Marking with ink marks, Rimbach (1898a) showed that the swollen root parts shorten in length by 50–70%. In *Acidanthera bicolor* (see Fig. 1), we found that 200-mm long swollen root parts contract by up to 80 mm. The ability to contract may occur within "normal" roots, which then have nutritional and contractional functions (see *Convallaria majalis* in Fig. 2). It should be mentioned that in this species the active roots are those at the tip of

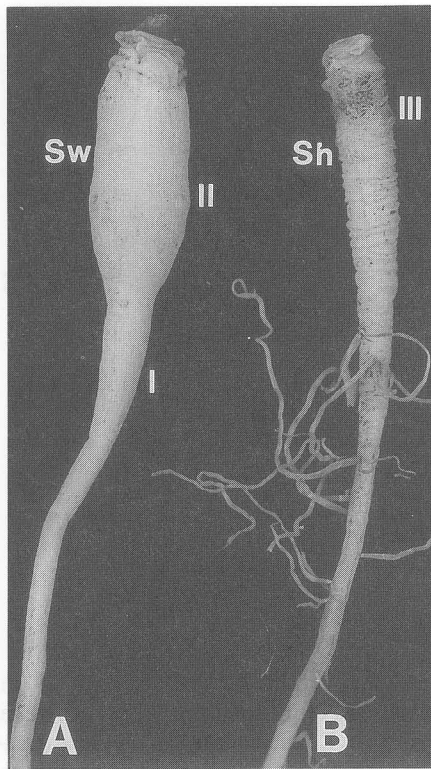


Figure 1 Contractile roots of *Acidanthera bicolor* at different stages of root age. (A) active root, (B) a root after contraction. Roman numerals indicate the different root zones. Sh, shrinkage; Sw, swelling (according to Pütz, 1990).

the rhizome; the wrinkled ones are old contractile roots after pulling activity which now function for nutrition. Other species show specialization and develop different roots, such as small ones for nutrition, and bigger, wrinkled roots for contraction (see *Tigridia pavonia* in Fig. 3).

Contractile roots can be interpreted as being transitory storage organs (Izuro and Hori, 1983c for *Oxalis bowieana* and *Gladiolus* sp.). However, in contrast to real storage organs, the store of materials is not used by the plant during the following vegetation period. Species with real storage roots may also show a contraction ability (e.g., *Hemerocallis fulva* in Fig. 10 or *Asphodelus* spp. [Cauro, 1968]). Such roots combine the functions of nutrition, contraction, and storage. Contraction occurs during the year of development, storage occurs later in the vegetation period, and in most cases is visible as a swollen distal root part. This storing capability is necessary for the survival of the plant for the next vegetation period. Turnips of many dicot species (e.g., *Trifolium pratense*, de Vries, 1877, 1880; *Heracleum sibiricum*, *Ferula glauca*, Berckmeyer, 1928) also seem to have a contraction ability. This contraction occurs on the proximal root parts, but also at the basal part of the shoot; for example, in the hypocotyl (see Rimbach, 1921a,b,c; Rauh, 1994).

Contractile roots are very useful in achieving movement of underground parts of an individual plant; for example, a corm, a bulb, or a rhizome. Movement of such organs occurs against soil resistance, and thus its degree depends on several soil parameters; for example, soil type, moisture, and density (Froebe and Pütz, 1988). Normally, if soil resistance becomes too high, no movement occurs. According to Kirschner et al. (1934), the function of root contraction could yield a better

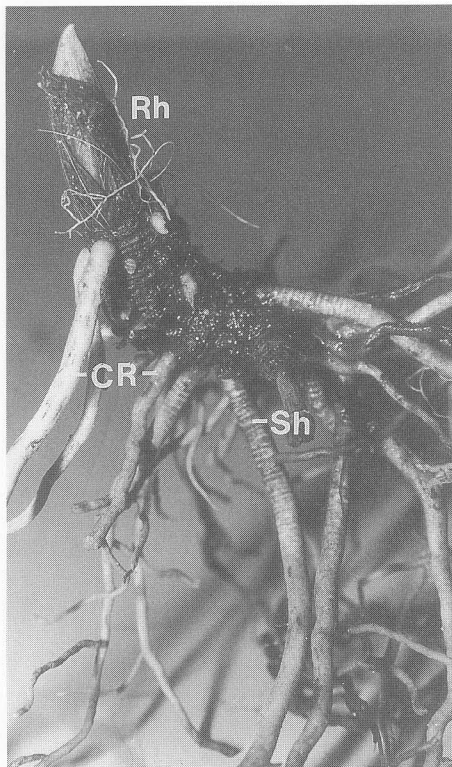


Figure 2 A rhizome of *Convallaria majalis* with contractile roots. Rh, rhizome; Sh, shrinkage; CR, contractile root.

anchorage of the individual plant (for root anchorage, cf. Ennos 1993; Ennos et al. 1993). It is interesting to note that even aerial roots of trees may be contractile (e.g., *Coussapoa schottii*, Nordhausen, 1913; *Ficus benjamina*, Zimmermann et al., 1968). Functioning like safetying ropes, aerial root contraction seems to be useful in achieving better stability of the individual plants.

II. REACTION MODES OF THE PLANT FOR AN UNDERGROUND MOVEMENT

A. Pulling Force of Contractile Roots

There is a requirement for the contractile roots to build up a pulling force for overcoming soil resistance for underground plant movement ("pull roots," Rimbach, 1898a; Duncan, 1925). This pulling force acts along the root axis toward the proximal as well as to the distal part of the root. In normal cases, however, the distal part of a root is anchored by root hairs or by lateral roots. Thus, pulling, created by root contraction, mainly effects the upper plant parts; for example, a bulb or a corm.

We quantified such a pulling force using two different methods—the direct lifting method (Pütz, 1992a) and the indirect experimental simulation (Pütz, 1992b). The lifting method is used with plants grown in a mist culture system. We fixed the plant organ on a stand and connected a single contractile root to a given mass. Root contraction creates a pulling force, which has to lift the mass up. This quantifies the pulling effect of a single contractile root (Pütz, 1992a):

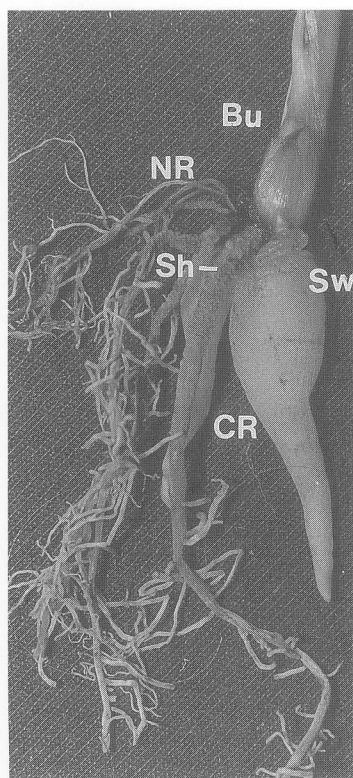


Figure 3 *Tigridia pavonia* bulb with contractile roots and nutritional roots. NR, nutrient roots; CR, contractile roots; Bu, bulb; Sw, swelling; Sh, shrinkage.

$$\text{Force or Weight (N)} = \text{mass (kg)} \times \text{acceleration (} = 9.81 \text{ m/s}^2 \text{)} \quad (1)$$

$$\text{Work (J)} = \text{Force (N)} \times \text{distance of lifting movement (m)} \quad (2)$$

$$\text{Power (W)} = \text{work (J)} : \text{pulling time (s)} \quad (3)$$

The second method measures the downward movement of a plant body in potted plants. Such a movement measures the total activity of all contractile roots of the plant. Standardization makes it possible to obtain some values for the pulling effect of the total number of contractile roots. By dividing the total force by the number of contractile roots, a value for a single contractile root can also be obtained by this indirect method. Both methods identify the quantity of work of a single contractile root as being of the same order of magnitude (Pütz, 1992a). Some values for force, work, and power of contractile roots are presented in Table 1. Most of the species are monocots, with *Oxalis pes caprae* being the only dicot whose contractile root has been measured to date.

B. Soil Channel Building by Contractile Roots (Pushing Force)

Thickening of root results in the soil being pushed laterally. During root contraction, a soil cavity appears that is equal in size to the root diameter. Many species develop contractile roots at the base of the plant body; thus, it is through the soil cavity that the plant organ can be transported with only a small expenditure of energy. Movement becomes greatly facilitated (Galil, 1969b, 1978, 1980). These cavities vary according to species, and Froebe and Pütz (1988) describe this property of the contractile root as the channel effect. This channel effect can be calculated in 10% steps (Pütz, 1992a).

Table 1 Average Values for the Activity of Single Contractile Roots of Different Plant Species

	F ^a	W ^b	P ^c
<i>Asphodelus aestivus</i> (Asphodelaceae) ^d	0.9	0.01	2.4
<i>Eucomis punctata</i> (Hyacinthaceae) ^e	1.5	0.03	2.9
<i>Sauromatum guttatum</i> (Araceae) ^{d,e}	1.2	0.01	3.3
<i>Tigridia pavonia</i> (Iridaceae) ^e	2.1	0.05	5.8
<i>Triteleia hyacinthina</i> (Alliaceae) ^d	0.9	0.01	3.1
<i>Oxalis pes-caprae</i> (Oxalidaceae) ^f	0.9	0.043	1.8

^aPulling force in (N).^bPulling force in (J).^cPulling power in ($W \times 10^{-9}$).^dPütz, 1992a.^ePütz, 1992b.^fPütz, 1994.

A root with a 100% channel effect (Fig. 4B) forms a channel through which the plant body can move free of any soil resistance (e.g., *Triteleia hyacinthina*, Smith, 1930, Pütz, 1992a; *Oxalis pes-caprae*, Galil, 1968a, Pütz, 1994; *Muscari parviflorum*, Galil, 1983a). In many species, the soil channel, thus formed, effects only parts of the plant body, and very often one can find a 10–20% channel created by relatively small contractile roots (e.g., *Scilla festalis*, Woodhead, 1904; *Allium ursinum*, Rimbach, 1897b). Larger contractile roots often create channels of approximate 40% and more (see Fig. 4A; e.g., *Tigridia pavonia*, *Strelitzia nicolai*, Pütz, 1992b). Soil resistance acts only on those parts of the plant body which are free of contractile roots. Simulation experiments were carried out in order to classify the role of a channel effect in terms of its energetic efficiency (Pütz et al., 1995). We found that, in general, formation of a channel saves a lot of work that would have been used for movement. This obvious statement becomes more significant when the very small amount of energy used in pushing is compared with the relatively high force needed for pulling. Thus, it becomes clear why only very few species, for example, *Amorphophallus bulbifer*, *Sauromatum guttatum* (Pütz, 1992a), and *Zantedeschia alba-maculata* show no channel effect.

With respect to natural conditions of the soil, it is clear that channel formation might be more efficient, not only from an energetic point of view but also from a functional one. For instance, in stony soils, a 100% channel formation may be the only possibility for a plant to move any of its organs or to overcome hindrances.

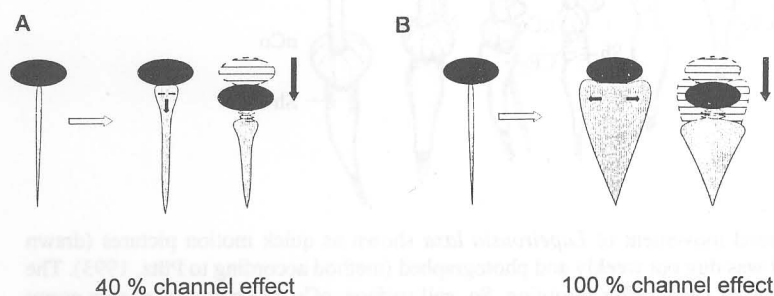


Figure 4 Schematic formation of soil channels by lateral push. Movement of the plant organ occurs in these cavities without soil resistance. (A) Diagram for building a smaller channel (40%). Lateral pushing of the soil and pulling are necessary to move the plant body through the soil. (B) Formation of a 100% channel. The push of the soil by the contractile root seems to be the most important for movement.

III. FUNCTION OF UNDERGROUND MOVEMENT

Ecologically oriented investigations into the survival of plants make clear that species are able to locate their underground parts in the desired sites. However, we found underground plant movement to be necessary in three respects, as discussed below.

A. Securing a Safe Position in the Soil

Geophytes have to survive cold winters or dry summers and thus very often show movements of their underground organs (bulbs, rhizomes, or corms) to regulate their depth. In this way, the individual plant can survive unfavorable seasons protected by an adequate amount of soil cover. In deeper soil positions, fluctuations in soil conditions (e.g., temperature, water) are smaller and conditions are closer to average. This means that plant organs buried deep in the soil are less likely to be subjected to drying or freezing during the dormancy period.

In earlier investigations, the movement was only assumed, an assumption based on the position of the plant body (cf. Rimbach, 1898a; Arber, 1925; Troll, 1937–1943; Galil, 1962, 1969a, 1980). Later, typical movements of monocotyledons were shown (Pütz, 1991), and *Nothoscordum inodorum* (Alliaceae) was the first bulbous plant whose underground movement was observed directly (Pütz, 1993). Typical movement in this species is tilting and twisting and reaches approximately 30–40 mm during one vegetation period.

Underground movements of certain plant organs are commonly achieved by the growth of such plant parts; for example, rhizomes, runners, or remoters (e.g., Arber, 1925; Raunkiaer, 1934; Troll, 1937–43; Galil, 1980). In cormous plants, for example, the Iridaceae, depth regulation often occurs by the contractile activity of roots but in combination with the growth of the shoot tip. A typical corm movement can be seen in *Lapeirousia laxa* (Fig. 5). Pulling of the first contractile root on only one side of the corm results in the old corm turning. Further contractile roots appear, pulling the underground plant organ downward. The new corm grows out at the side of the old one, and normally has a sloping position (see Fig. 8; Troll, 1937–1943). In some cases, downward movement can be counteracted by the growing activity of the new corm, which in extreme cases, can work in the opposite direction (e.g., *Sauromatum guttatum*, *Hemerocallis fuva*, see Figs. 9 and 10). To secure an

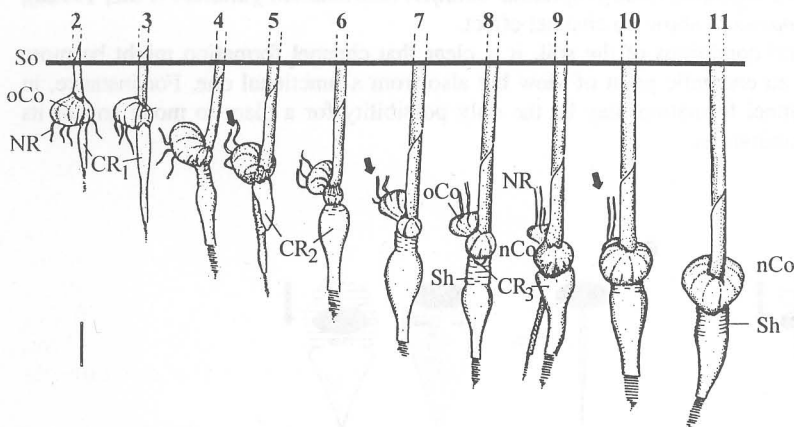


Figure 5 Typical underground movement of *Lapeirousia laxa* shown as quick motion pictures (drawn from photos). The individual was dug out weekly and photographed (method according to Pütz, 1993). The headline represents the number of weeks after sprouting. So, soil surface; oCo, old corm; nCo, new corm; NR, nutrient roots; Sh, shrinkage; CR, contractile root (indices shows successive development). Arrow shows secondary change of the course of NR caused by continuous corm movement. Bar represents 1 cm. (Modified from Pütz, 1992c.)

underground position, it is necessary to compensate for the upward growth of vertical corms. Direct observation in *Sauromatum guttatum* shows that a defined position is maintained, or that small downward movement of adult corms occurs through the activity of contractile roots (Pütz, 1996).

Orientation of axis growth into the direction of contractile root activity results in the addition of the effects of both components. This can be seen in *Lapeirousia*, but is well established in species having horizontal corms (e.g., *Arum* sp., Rimbach, 1897a).

The total amount of moving work, in relation to channel width and moving distance (Pütz et al., 1995) characterizes, from an energetic point of view, an optimum system of movement with small channels (10–40%); seemingly this is efficient for short distances (up to 30 mm). Many monocot species have contractile roots which produce small channels (10–40%). Such species show only a slight underground movement (10–40 mm, Pütz, 1992b) necessary, for example, to compensate for shoot growth of the vertical corm.

However, there are some indications that plants having their underground organs located near the soil surface are able to increase their channel effect partly by increasing root diameter (*Phaedranassa chloracea*, Rimbach, 1938) and partly by reducing the diameter of the bulb or corm (*Crocus sativus*, Negbi et al., 1989).

An increase in the channel effect results in the second energetic moving system (Pütz et al., 1995): For movements over greater distances (e.g., 50 mm and more), the 100% channel is superior. However, 100% channels are comparatively rare. The movement of turnips of the Apiaceae, which seem to be contractile (Berckemeyer, 1928) and have a diameter of 30 mm and more, can be interpreted in this way.

Shallow planted individuals of *Arisarum vulgare* (Galil, 1978) have a rather special moving system as a combination of shoot growth and root contraction. For the roots to achieve a 100% channel effect, the creation of a space in the soil, through which the elongated corm (remoter) advances (pioneer roots, Galil, 1969b, 1978), seems to be most common. The innovation buds of the corm can reach deeper positions in the soil of up to 80 mm. It is interesting to note that the corm changes its shape to a thick corm on reaching a “physiological” depth (Galil, 1958).

B. Vegetative Spreading of Daughter Bulbs or Corms

In many cases, the mother plant creates lateral buds, which develop into daughter corms or bulbs and become separated. Over several years, large underground aggregates of bulbs or corms appear in such species. Many species develop contractile roots from these lateral buds. Contractile root(s) activity results in a movement of the lateral buds away from the mother plant. Very often this vegetative spreading, visible in *Nothoscordum inodorum* (Pütz, 1993), extends only a few millimeters from the mother bulb.

Contractile roots with a 100% channel that enable movement of a rather greater distance can be observed in several species. *Triteleia hyacinthina* (Smith, 1930; Pütz, 1992a) has big contractile roots only on the small lateral corms, which become separated in the horizontal direction by root activity over a distance of 4–10 cm. *Oxalis pes-caprae* has a very special moving system (Pütz, 1994). This is produced by a combination of root contraction and a few basal internodes of the shoot which elongate to form a thin underground axis (Fig. 6), which can be designated a “thread” (Galil, 1968a). Along this thread, several renewal bulbs appear over a length of approximately 20–30 cm (–47 cm, Galil, 1968a). Although in both species a 100% channel appears, the roots still create a comparable pulling force (see Table 1).

In most cases, the direction of contractile roots is downward so that a deeper soil position for the plant organ is reached. Vegetative spreading also makes the horizontal direction useful. Galil (1968a) pointed out that in shallow planted individuals of *Oxalis*, the direction of the root is downward. However, plants having obtained their physiological depth develop roots in a horizontal direction, so that vegetative dispersal also becomes horizontal. Other examples with horizontal contractile roots are, for example, *Gynandris sisyrinchium* and *Muscari parviflorum* (Galil, 1980, 1981, 1983a), which aid the vegetative spreading in many cases together with a remoter.

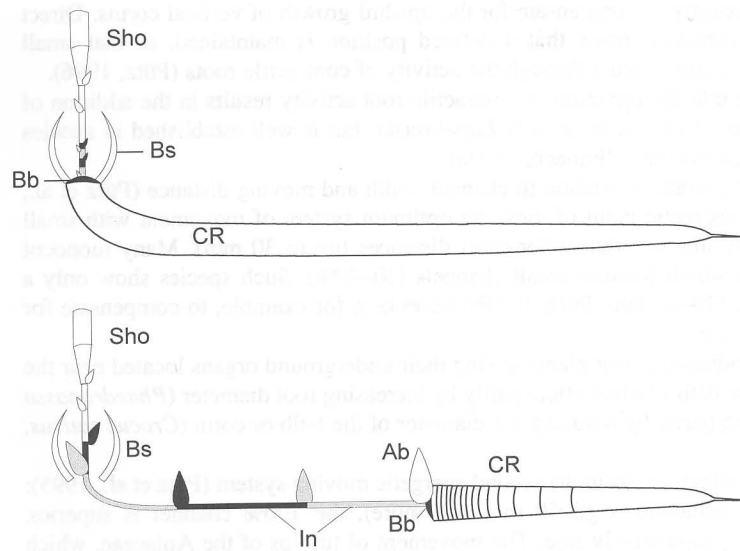


Figure 6 *Oxalis pes-caprae*; schematic presentation of the underground movement by root contraction and shoot elongation. The elongating internodes are colored gray and black. Cross lines on the contractile root indicate contraction. Ab, axillary bud, subsequently the new bulb; Sho, aboveground shoot; Bs, scales of the old bulb; Bb, bottom of the old bulb; In, internode; CR, contractile root. (Modified from Pütz, 1994.)

C. Achieving an Ecologically Useful Position

Seeds germinate beneath the soil surface. For survival of the perennial organs, it is necessary for them to reach a safe position in the soil. In many species, this is made possible by elongation of the cotyledon. Sometimes seedling penetration becomes more specialized; for example, cases where a tube is built up from the primary root (e.g., *Oxalis rubella*, Troll 1937–1943; *Colchicum stevenii*, Galil, 1968b; *Ixiolirion tataricum*, Galil, 1983b).

Downward movement of the seedling is also caused by contractile root activity. It is known that in many species (e.g., *Lilium martagon*, *Scilla festalis*, *Arum maculatum*, *Romulea bulbocodium*,

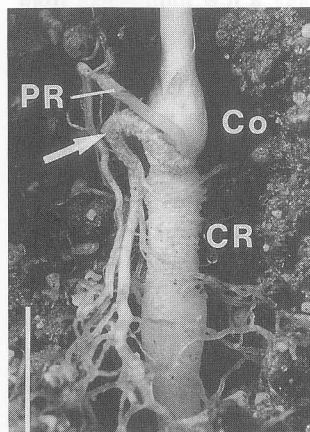


Figure 7 Eight-week-old seedling of *Lapeirousia laxa*. Co, corm; CR, contractile root; PR, primary root. The course of the first roots has already changed due to the continuous movement (arrow). Bar represents 1 cm.

Lapeirousia laxa, Fig. 7), the primary root and the first adventitious roots are contractile (Rimbach, 1898b; Arber, 1925; Kirchner et al., 1934; Bussen, 1951). Jernstedt (1984) has observed downward movement with *Chlorogalum pomeridianum* seedlings of some 64 mm over a period of 29 weeks. We have recorded the downward movement of *Nothoscordum inodorum* in quick motion pictures (Pütz, 1993), reaching a depth of 75 mm over a 35-week period. Large movements are enabled by the pulling force of the contractile roots as well as by their pushing effect. The channel build-up in the case of seedlings often reaches 100%. Thus, a small plant body can be moved with less soil resistance. From an ecological standpoint, seedling penetration is the most important underground movement, since it allows the seedlings to settle into their proper position. Seedlings of geophytes reach a safe position during the first weeks and can thus survive the first unfavorable season.

IV. INDUCTION OF CONTRACTILE ROOTS

Shallow planted plants, even in their adult stage, very often produce contractile roots and are able to show underground movement. However, deep planted individuals of several species seem to register their position and, when satisfied, produce no more contractile roots (e.g., Rimbach, 1897a,b, 1938; Kirchner et al., 1934; Iziro and Hori, 1938b; Halevy, 1986). Galil (1958) was the first to find a parameter responsible for soil position registration with *Leopoldia maritima*—the only factor seems to be rapid fluctuations of soil temperature. Iziro and Hori (1983a) confirmed those temperature effects with *Gladiolus* and *Oxalis bowieana*. Another parameter influencing contractile root development in *Gladiolus* is an illumination of the sheath leaves (Jacoby and Halevy, 1970; Halevy, 1986).

Underground movement of geophytes can be completely understood only if the induction of contractile root activity is classified. We have carried out some examinations, not with species which have different root types (nutritional roots and contractile ones, e.g., *Leopoldia maritima*, *Gladiolus* sp. or *Lapeirousia laxa* in Fig. 8), but with species having only one type of root (e.g., *Nothoscordum inodorum* [Pütz, 1993], *Sauromatum guttatum* in Fig. 9 and *Hemerocallis fulva* in Fig. 10). To

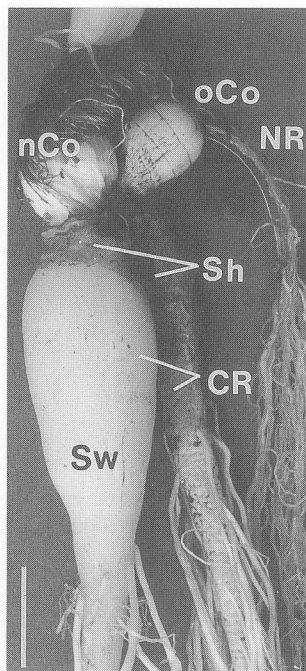


Figure 8 *Lapeirousia laxa* adult corm with contractile roots and nutritional ones. NR, nutrient roots; CR, contractile roots; Co, corm (o, old one; n, new one); Sw, swelling; Sh, shrinkage. Bar represents 1 cm.

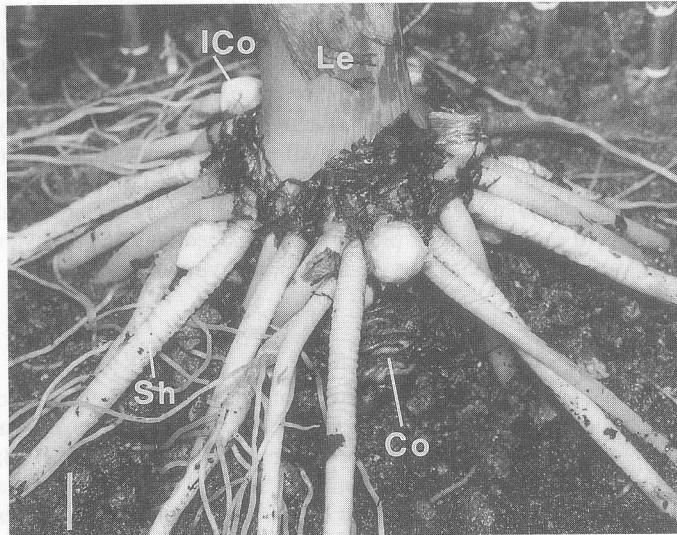


Figure 9 *Sauromatum guttatum* adult corm with roots developing at the top of the corm. The roots function for nutrition and contraction. Sh, shrinkage; Co, corm; ICo, lateral corm; Le, leaf (petiole). Bar represents 1 cm. (From Pütz, 1991.)

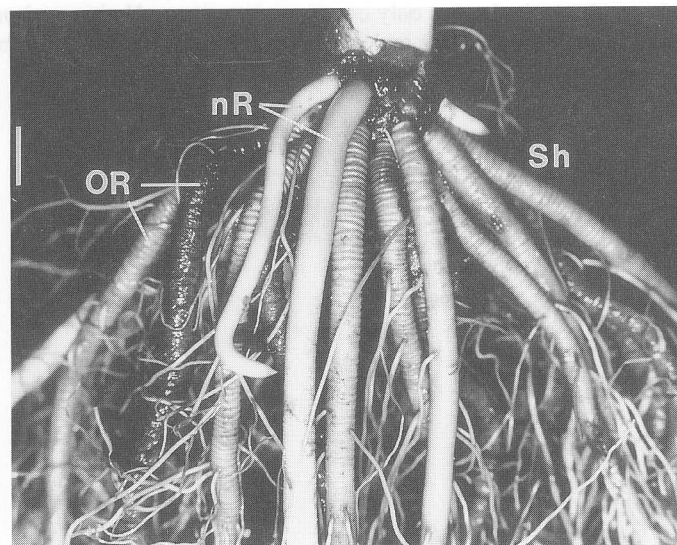


Figure 10 *Hemerocallis fulva* vertical corm with roots which initially function for nutrition and contraction. Later they store for the next vegetation period. Sh, shrinkage; nR, roots of this vegetation period; oR, old roots, developed in the last vegetation period. Bar represents 1 cm.

quantify the activity of contractile roots in such species, their pulling work must be measured using the lifting method.

From our present knowledge, it is clear that several factors can influence contractile root activity: In *Nothoscordum inodorum*, illumination of the basal leaf parts seems to be the only factor. In *Sauromatum guttatum*, the same applies, although high day-night temperature changes in the last vegetation period form a second parameter, which induces lower contractile root activity. In our species, the main parameter seems to be light illumination on the sheath leaves. Up to now, we have found no effects on contractile root activity due to temperature changes during the growing season.

V. ANATOMICAL FEATURES OF CONTRACTILE ROOTS OF MONOCOTYLEDONS

Most reports in the literature that deal with root contraction have been based on the structural aspects of the mechanism. For monocotyledons, the active mechanism has been discussed with respect to interesting anatomical details. Several anatomical changes appear in the roots as a result of its shortening. Such anatomical patterns allow the distinction of different types of root contraction within the monocotyledons.

A. Storey-Collapsing Type

Longitudinal sections of contractile roots of a few monocotyledons show a characteristic feature of layers of collapsed cortex cells arranged in storeys together with a spirally undulated stele (see scheme in Fig. 11A). Before root contraction takes place, the stele appears straight. This type can be found in *Brodiaea lactea* (Smith, 1930; Thoday, 1931), *Dichelostemma* sp. and *Triteleia* sp. (Tribus *brodiaea* of the subfamily Alliioideae), and perhaps in some orchid roots; for example, in *Dactylorhiza maculata* (Kirchner et al., 1934). The cortex cells increase in a radial and tangential direction by a combination of growth and turgor, whereas simultaneously decreasing in length (Smith, 1930). Smith (1930) concludes that the active cell shortening leads to longitudinal tension which is compensated by collapsing of the cells and spiraling of the stele.

B. Ring-Collapsing Type

The contracted roots of most monocotyledons show another pattern of features (see Fig. 11B,C). Apparently a ring of collapsed cells is situated beneath the exodermis. This is most obvious in cross section through zone III (see Fig. 11C). Moreover, in most cases, one can find radially expanded cortical cells; for example, in *Crinum capense*, *Gladiolus* sp., *Hyacinthus orientalis*, *Arum italicum*,

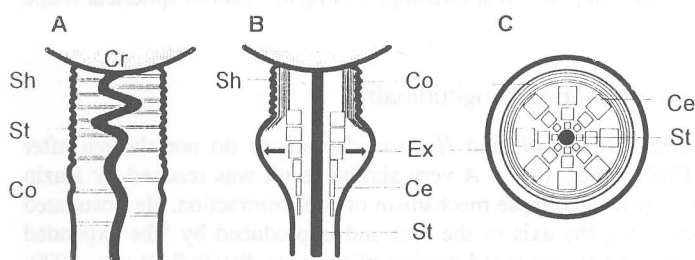


Figure 11 Schematic patterns of root contraction: (A) longitudinal section of a root showing the storey-collapsing type. (B) longitudinal section of a root showing the ring-collapsing type. (C) Cross section of a contractile root in zone III showing the ring-collapsing type. Co, collapsing cells; Ce, cortical cells; Ex (arrow), expansion; Cr, cryptocorm (e.g., bulb or corm); Sh, shrinkage; St, stele. (Figs. A and B from Pütz and Froebe, 1995.)

Narcissus pseudonarcissus, *Allium polyanthum*, and *Chlorogalum pomeridianum* (Gravis, 1926; Pfeiffer, 1931; Wilson and Honey, 1966; Lamant and Heller, 1967; Chen, 1969; Deloire, 1980; Jernstedt, 1984a).

It is generally believed that the macroscopic feature of contractile roots, wrinkling of the root surface and compression of the stele, are passive reactions to the shortening process within the root. Compression of the stele is not a macroscopic feature and thus not visible in Fig. 11B. Features of a passive compression can be seen from the turns of the spirals of metaxylem vessels being closer together or from the minute wavy folds of the longitudinal walls of individual cells (cf. Wilson and Honey, 1966; Chen, 1969; Jernstedt, 1984a).

Apparently, the cells of the root cortex seem to be responsible for the active shortening process. There are two opinions concerning the exact localization of the active layers and the changes which occur in cell dimension.

1. Cells of the Root Cortex Expand Radially While They Shorten Longitudinally

Such changes were found by comparing sections of contracted parts of the roots with those of noncontracted parts. However, only a few reports in the literature present comprehensive measurements of such cells (e.g., Deloire, 1980; Jernstedt, 1984a). Localization of the active cells is implied from the cross sections, where the radial expansion of the cortex cells seems to reflect their shortening activity. This activity was described as starting at the middle, possibly together with parts of the outer cortical cells, and afterwards spreads continuously to the inner cortex cells (Lamant and Heller, 1967; Jernstedt, 1984a). After expansion, the active cells collapse. Other investigators have described the inner cortical cells as being active in expansion and shortening, whereas the outer cells have collapsed (Wilson and Honey, 1966; Chen, 1969; Reynecke and van der Schijff, 1974; Deloire, 1980).

This inconsistency in active cell layer localization probably results from different times of observation. Examination of young active roots (zone II in Fig. 1A) shows outer and middle cortical cells expanding and shortening, whereas older roots (zone III in Fig. 1B) show the outer and middle cortical cells collapsed with changes in the inner cells. This can easily be verified with *Narcissus tazetta* and *Hyacinthus orientalis* roots using some hand cuts of various old contractile roots.

Wilson and Honey (1966) have done some ultrastructure examinations of the cell walls and postulate a reorientation of cell growth from the normal longitudinal extension growth to a radial expansion (Wilson and Anderson, 1979; Jernstedt 1984b). The changing anisotropy in the extensibility of cell walls or, more simply, the active growth of upper and lower walls together with vertical radial walls growing at a lower pace lead to cells automatically shortening during radial expansion: "The radial extension would necessarily tend to produce a vertical shortening of these walls" (Wilson and Honey, 1966, p. 59). Chen (1969), in accordance with de Vries (1880), does not exclude the participation of turgor pressure in the first phase of shortening, leading to a shorter spherical shape of the isotropic cell.

2. Expanding Cortical Cells Do Not Shorten Longitudinally

Radially expanded cells of *Cooperia drummondii* and *Hypoxis decumbens* do not shorten after expanding but collapse (Church, 1919; Arber, 1925). A very similar result was reached by Ruzin (1979), which lead him to describe a growth/collapse mechanism of root contraction. He postulated that a longitudinal tension develops along the axis of the root and is produced by "the expanded diameter of the root contiguous with the non-expanded portion of the root distally" (Ruzin, 1979; Burström, 1971). The outer cortex cells have an important function as buffer, because the successive collapse of these cells keeps the longitudinal tension constant over a longer period. The inner cortex cells shorten comparably, which is necessary to compensate for the longitudinal tension. As Ruzin detects a partial dissolution of the middle lamellar material of the innermost cortex cells, he interpreted their shortening as being passive.

C. Contractile Root Maceration

One reason for the different view concerning the mechanism of root contraction in monocotyledons is that the continuity of shortening has not really been taken into account. A qualitative description of cell changes is not sufficient and semiquantitative measurements in serial cuts are problematic. It hardly seems possible to make cuts which are parallel to the vertical walls of the cells, in particular through the inner cortical cells, which are very long but very thin. According to Jernstedt (1984a), the inner cortical cells in *Chlorogalum pomeridianum* reach a size of $680 \times 25 \mu\text{m}$. Nonparallel cuts result in cells being arbitrarily cut off and in measured cell dimensions of dubious reliability. A reliable method is by tissue maceration, which was first used by Deloire (1980). Later the "maceration method" of Pütz et al. (1990) made it possible to measure the cell dimension of just about every tissue sample of the root. Measurements made with *Acidanthera bicolor* (Iridaceae) showed that the middle and outer cortical cells expand and collapse but without any shortening (type 2). We have done further investigations with *Arisarum vulgare* (Pütz and Froebe, 1995) which show that the outer and middle cortical cells expand radially (increase in volume: cell growth) with simultaneous longitudinal shortening and finally collapse (type 1). This contradicts the "transversal-contractile pioneer roots" hypothesis of Galil (1978). 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 of *Arisarum* occur at different times. Then, first a radial expansion of the cells is seen, followed by their shortening.

Based on the data for *Acidanthera* and *Arisarum*, we suggest a unified anatomical model of root contraction within the ring-collapsing type (Pütz and Froebe, 1995). In this model, radial expansion and longitudinal shortening are regarded as 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, we assume that the inner cortical cells shorten actively and thus produce a pulling force. Such a shortening or pulling activity can be limited to the inner cells (e.g., in *Acidanthera*), but very often 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 radial expansion, which is not immediately connected with root shortening! Radial expansion develops a force which pushes the soil sideward and enables an easier movement in the soil (channel effect). These cells become passively compressed by the pulling activity of the inner cells. The collapse of these cells promotes shortening passively.

By postulating an active shortening of the inner cortical cells, the main aspect of root contraction can be seen in a new light: What is the contractile element? To answer the question as to how the active shortening occurs intracellularly, one has to assume that shortening occurs at a constant cell volume. This means that cell growth (as mentioned by cf. Wilson and Honey, 1966; Jernstedt, 1984a, etc.) cannot be responsible for contraction! Other explanatory factors could be the position and orientation of fibrils, microtubules, or special elements within the longitudinal cell walls. However, earlier investigations into the position and orientation of fibrils and microtubules in cortical cell walls of contractile roots were based on the belief that the cell grows (Cyr et al., 1988; Lin and Jernstedt, 1988; Smith-Huerta and Jernstedt, 1989, 1990). It remains unclear whether the fibrils which change during contraction are part of an active process or are just a passive reaction to equalize an axial tension. Therefore, they cannot produce a satisfactory explanation of the intracellular mechanism of root contraction.

VI. ANATOMICAL FEATURES OF ROOT SHORTENING IN DICOTYLEDONS, GYMNOSPERMS, AND FERNS

Drawing an overall picture of the contraction is possible in principle for monocotyledons but is impossible for dicotyledons. Not much work has been done with such plants. In Oxalidaceae, the storey-collapsing type seems to exist (Thoday, 1926; Rohde, 1928; Thoday and Davey, 1932; Davey, 1946). In contracting roots and stems of cycads (e.g., *Cycas revoluta*), where contraction

results from cell row collapse, similar features were reported (Watanabe, 1925; Stevenson, 1980). According to Stevenson (1975), such a contraction mechanism even occurs in *Botrychium multifidum* (Ophioglossaceae).

In plants of the Apiaceae, expanding cells push against resin vessels and thus produce a longitudinal tension (Berckemeyer, 1928). Local expansion can also be found in the roots (and the hypocotyl) of *Melilotus alba* (Bottum, 1941). A very special behavior of root contraction was described in *Incarvillea delavayi* (Rimbach, 1921c), where the turnip seems to build up a new cortex parenchyma at every vegetation period. Cells of this new cortex are contractile. This would mean that contractile roots of *Incarvillea* might be the only ones with regularly recurring contraction. The most recent report concerning root contraction in dicots is that of Zamski et al. (1983), who describe the contraction of roots in *Gymnarrhena micranatha*. They found that the active cells are those of the endodermis, of the pericycle, and of the primary phloem, which expand radially while shortening longitudinally. Such features are very close to those of the ring-collapsing type.

VII. CONCLUSIONS

The movement of an underground plant body as effected by contractile roots seems to be generally understood. Up to the present, investigations have been concerned with underground movement behavior and contractile root induction. However, further examination of these topics would prove useful, especially when related to seedlings, and including more ecological aspects of underground movement and of the soil-plant relationship. This would provide us with better knowledge about the contribution of contractile roots to the survival of the plants in their respective environments.

Investigations about developmental physiology are totally lacking. Nothing is known about the control mechanism causing a root to contract or signal perception, storing, and processing. If we consider the function of individual anchorage, there is a total lack of information regarding the contribution of such roots to tree stability, especially in connection with the traits of aerial roots. Ecological, anatomical, and biomechanical examinations are needed in this field. Finally, anatomical features of root contraction still require our attention in three different respects:

1. The changes that occur within the ring-collapsing type at the intracellular level and the main question, which is of what does the contractile element consist?
2. In the storey-collapsing type, the anatomical features have not been described in detail, and quantitative measurements of cell dimensions are still lacking. Thus, nothing is known about where the active contractile parts in the roots are located and how the force is created. Therefore, comparative studies of monocotyledons (Allioideae), dicotyledons (Oxalidaceae), gymnosperms (Cycadaceae), and ferns (Ophioglossaceae) are needed.
3. Root contraction in other dicot families remain fully unexplored. Anatomical examinations of such roots are necessary, including the features of hypocotyl contraction and of the secondary thickening.

REFERENCES

- Arber, A. (1925). *Monocotyledons—A Morphological Study*. Cambridge University Press, Cambridge, UK.
- Berckemeyer, W. (1928). Über kontraktile Umbelliferenwurzeln. *Bot. Archiv.* 24: 273–318.
- Bottum, F. R. (1941). Histological studies on the roots of *Melilotus alba*. *Bot. Gaz.* 103: 132–145.
- Burström, H. G. (1971). Tissue tensions during cell elongation in wheat roots and a comparison with contractile roots. *Physiol. Plants* 25: 509–513.
- Bussen, M. (1951). Untersuchungen über die Bewurzelung der Keimpflanzen im Verwandtschaftskreis der Monokotylen. Ph.D. dissertation, Universität Mainz, Mainz, Germany.
- Cauro, R. (1968). Introduction à la biologie d'une Asphodèle, *L'infor. Scient.* 5: 215–224.
- Chen, S. (1969). The contractile roots of *Narcissus*. *Ann. Bot.* 33: 421–426.
- Church, M. (1919). The development and structure of the bulb in *Cooperia drummondii*. *Bull. Torrey Bot. Club* 46: 337–362.

- Cyr, J. R., Lin, B. L., and Jernstedt, J. A. (1988). Root contraction in hyacinth. II. Changes in tubulin levels, microtubule number and orientation associated with different cell expansion. *Planta* 174: 446–452.
- Dahlgren, R. M. T., Clifford, H. T., and Yeo, P. F. (1885). The families of the monocotyledons. Structure, evolution, and taxonomy. Springer, Berlin.
- Davey, A. J. (1946). On the seedling of *Oxalis hirta* L. *Ann. Bot. NS* 39: 237–256.
- Deloire, A. (1980). Les racines tractrices de l'*Allium polyanthum* Roem. et Schult: une étude morphologique, anatomique et histoenzymologique. *Rev. Cytol. Biol. Veget. Bot.* 3: 383–390.
- de Vries, H. (1877). Beiträge zur speziellen Physiologie landwirtschaftlicher Kulturpflanzen. Wachstums-geschichte des rothen Klees. *Landwirtschaftl. Jahrb.* 6: 893–1076.
- de Vries, H. (1880). Ueber die Kontraktion der Wurzeln. *Landwirthschaftl. Jahrb.* 9: 37–95. In Hugo de Vries, *Opera e Periodicis collata*. Vol. II, Utrecht, The Netherlands, A. Oosthoek, MCMXVIII.
- Duncan, J. F., (1925). "Pull roots" of *Oxalis esculenta*. *Trans. Bot. Soc. Edinb.* 29: 192–196.
- Ennos, A. R. (1993). The scaling of root anchorage. *J. Theoret. Biol.* 161: 61–75.
- Ennos, A. R., Crook, M. J., and Grimshaw, C. (1993). A comparative study of the anchorage systems of himalayan balsam *Impatiens glandulifera* and mature sunflower *Helianthus annuus*. *J. Ex. Bot.* 44: 133–146.
- Froebe, H. A., and Pütz, N. (1988). Orientierende Versuche zur Verlagerung pflanzlicher Organe im Erdboden durch definierte Kräfte. *Beitr. Biol. Pflanzen* 63: 81–100.
- Galil, J. (1958). Physiological studies on the development of contractile roots in geophytes. *Bull. Res. Council. Isr.* 6: 223–236.
- Galil, J. (1962). Development cycle and ecology of *Iris palestina* (Bak.). *Boiss. Bull. Res. Council. of Isr.* 11: 17–24.
- Galil, J. (1965). Vegetative dispersal of *Allium neapolitanum*. *Am. J. Bot.* 52: 282–286.
- Galil, J. (1968a). Vegetative dispersal in *Oxalis cernua*. *Am. J. Bot.* 55: 68–73.
- Galil, J. (1968b). Biological studies on the seedling of *Colchicum stevenii* Kunth. *Beitr. Biol. Pflanzen* 45: 243–256.
- Galil, J. (1969a). Morpho-ecological studies on *Gladiolus segetum* Gawl. *Isr. J. Bot.* 18: 43–54.
- Galil, J. (1969b). On the laterally-contracting root of *Colchicum stevenii*. *Beitr. Biol. Pflanzen* 46: 315–322.
- Galil, J. (1978). Morpho-ecological studies on *Arisarum vulgare* Targ.-Tozz. *Isr. J. Bot.* 27: 77–89.
- Galil, J. (1980). Kinetics of bulbous plants. *Endeavour* 5: 15–20.
- Galil, J. (1981). Morpho-ecological studies on geophilic plants. Vegetative dispersal of *Gynandiris sisyrinchium* L. *Isr. J. Bot.* 30: 165–172.
- Galil, J. (1983a). Vegetative dispersal of *Muscari parviflorum* Desf. *Isr. J. Bot.* 32: 221–230.
- Galil, J. (1983b). Morpho-ecological studies of lowering in the seedling of the geophyte *Ixiolirion tataricum* (Pall.) Herb. *New Phytol.* 143: 143–150.
- Gravis, A. (1926). Contribution a l'étude anatomique du raccourcissement des racines. *Acad. R. Belgique Bull. Cl. Sci.* 12: 48–69.
- Halevy, A. H. (1986). The induction of contractile roots in *Gladiolus grandiflorus*. *Planta* 167: 94–100.
- Izuro, Y., and Hori, Y. (1983a). Effect of temperature on the growth of contractile root(s) of daughter corm or bulbs in *Gladiolus* and *Oxalis bowieana* Lodd. *J. Jpn. Soc. Hort. Sci.* 51: 459–465.
- Izuro, Y., and Hori, Y. (1983b). Effect of planting depth on the growth of contractile root(s) of daughter corm or bulbs in *Gladiolus* and *Oxalis bowieana* Lodd. *J. Jpn. Soc. Hort. Sci.* 52: 51–55.
- Izuro, Y., and Hori, Y. (1983c). Retranslocation of photoassimilates accumulated in contractile root(s) to daughter corm or bulbs in *Gladiolus* and *Oxalis bowieana* Lodd. *J. Jpn. Soc. Hort. Sci.* 52: 56–64.
- Jacoby, B., and Halevy, A. H. (1970). Participation of light and temperature fluctuations in the induction of contractile roots of *Gladiolus*. *Bot. Gaz.* 131: 74–77.
- Jernstedt, J. (1984a). Seedling growth and root contraction in the soap plant, *Chlorogalum pomeridianum* (Liliaceae). *Am. J. Bot.* 71: 69–75.
- Jernstedt, J. (1984b). Root contraction in hyacinth. I. Effects of IAA on differential cell expansion. *Am. J. Bot.* 71: 1080–1089.
- Kirchner, O., von, Loew, E., and Schröter, C. (1934). Lebensgeschichte der Blütenpflanzen Mitteleuropas. Spezielle Ökologie der Blütenpflanzen Deutschlands, Österreichs und der Schweiz. Band 1.3 and 1.4, Ulmer, Stuttgart.
- Lamant, A., and Heller, R. (1967). Sur la Contraction des Racines d'*Arum italicum*. *Bull. Soc. Franc. Physiol. Veget.* 13: 179–193.
- Lin, B. L., and Jernstedt, J. (1988). Microtubule organization in root cortical cells of *Hyacinthus orientalis*. *Protoplasma* 141: 13–23.
- Negbi, M., Dagan, B., Dror, A., and Basker, D. (1989). Growth, flowering, vegetative reproduction, and dormancy in the saffron crocus (*Crocus sativus* L.). *Isr. J. Bot.* 38: 95–113.
- Nordhausen, M. (1913). Über kontraktile Luftwurzeln. *Flora* 105: 102–126.
- Pfeiffer, N. E. A. (1931). Morphological study of *Gladiolus*. *Contrib. Boyce-Thompson Inst.* 3: 173–195.
- Pütz, N. (1991). Die Zugbewegungstypen bei den Monokotylen. *Bot. Jahrb. Syst.* 112: 347–364.
- Pütz, N. (1992a). Measurement of the pulling force of a single contractile root. *Can. J. Bot.* 70: 1433–1439.

- Pütz, N. (1992b). Das Verhältnis von Bewegung und Wurzelkraft bei Monokotylen. *Beitr. Biol. Pflanzen* 67: 173–191.
- Pütz, N. (1992c). Underground movement by contractile roots. In *Root Ecology and Its Practical Application*, 3. (L. Kutschera, E. Hübl, L. Lichtenegger, H. Persson, and M. Sobotik, Eds.). ISRR Symposium, Vienna, 1992 pp. 669–672.
- Pütz, N. (1993). Underground plant movement. I. The bulb of *Nothoscordum inodorum* (Alliaceae). *Bot. Acta* 106: 338–343.
- Pütz, N. (1994). Underground plant movement. II. Vegetative spreading of *Oxalis pes-caprae* L. *Plant Syst. Evol.* 191: 57–67.
- Pütz, N. (1996). Underground plant movement. III. The corm of *Sauromatum guttatum* (Araceae). *Flora* (in press).
- Pütz, N., and Froebe, H. A. (1995). A re-evaluation of the mechanism of root contraction in Monocotyledons using the example of *Arisarum vulgare* Targ.-Tozz. (Araceae). *Flora* 190/3: 285–297.
- Pütz, N., Froebe, H. A., and Haese, U. (1990). Quantitative Untersuchungen zum Mechanismus der Wurzelkontraktion bei *Acidanthera bicolor* Hochst. (Iridaceae). *Beitr. Biol. Pflanzen* 65: 147–161.
- Pütz, N., Hüning, G., and Froebe, H. A. (1995). Cost and advantage of soil channel formation by contractile roots in successful plant movement. *Ann. Bot.* 75: 633–639.
- Rauh, W. (1994). *Morphologie der Nutzpflanzen*. Reprint of 2nd edition, 1950. Quelle & Meyer, Heidelberg.
- Raunkiaer, C. (1934). *The life forms of plants and statistical plant geography*. Clarendon, Oxford, UK.
- Reyncke, W. F., and van der Schijff, H. P. (1974). The anatomy of contractile roots in *Eucomis* L'Hérit. *Ann. Bot.* 38: 977–942.
- Rimbach, A. (1897a). Ueber die Lebensweise des *Arum maculatum*. *Ber. Deutsch. Bot. Ges.* 15: 178–182.
- Rimbach, A. (1897b). Lebensverhältnisse des *Allium ursinum*. *Ber. Deutsch. Bot. Ges.* 15: 248–252.
- Rimbach, A. (1898a). Die kontraktile Wurzeln und ihre Thätigkeit. *Beitr. zur wissenschaftl. Botanik* 2: 1–26.
- Rimbach, A. (1898b). Über *Lilium marthagon*. *Ber. Deutsch. Bot. Ges.* 16: 104–110.
- Rimbach, A. (1921a). Über die Wachstumsweise der Wurzel von *Incarvillea Delavayi*. *Ber. Deutsch. Bot. Ges.* 39: 288–290.
- Rimbach, A. (1921b). Über Wurzelverkürzung bei dicotylen Holzgewächsen. *Ber. Deutsch. Bot. Ges.* 39: 281–284.
- Rimbach, A. (1921c). Über die Verkürzung des Hypocotyls. *Ber. Deutsch. Bot. Ges.* 39: 285–287.
- Rimbach, A. (1926a). Die Größe der Wurzelverkürzung. *Ber. Deutsch. Bot. Ges.* 14: 328–334.
- Rimbach, A. (1926b). Über Verkürzung von Stengeln. *Ber. Deutsch. Bot. Ges.* 44: 335–338.
- Rimbach, A. (1927). Die Geschwindigkeit und Dauer der Wurzelverkürzung. *Ber. Deutsch. Bot. Ges.* 45: 127–130.
- Rimbach, A. (1929). Die Verbreitung der Wurzelverkürzung im Pflanzenreich. *Ber. Deutsch. Bot. Ges.* 47: 22–31.
- Rimbach, A. (1938). *Phaedranassa chloracea*. *Ber. Deutsch. Bot. Ges.* 56: 440–446.
- Rohde, H. (1928). Über die kontraktile Wurzeln einiger Oxalidaceen. *Botan. Archiv* 22: 463–532.
- Ruzin, S. (1979). Root contraction in *Freesia* (Iridaceae). *Am. J. Bot.* 66: 522–531.
- Smith, F. H. (1930). The corm and contractile roots of *Brodiaea lactea*. *Am. J. Bot.* 17: 916–927.
- Smith-Huerta, N. L., and Jernstedt, J. A. (1989). Root contraction in hyacinth. III. Orientation of cortical microtubules visualized by immunofluorescence microscopy. *Protoplasma* 151: 1–10.
- Smith-Huerta, N. L., and Jernstedt, J. A. (1990). Root contraction in hyacinth. IV. Orientation of cellulose microfibrils in radial, longitudinal and transverse cell walls. *Protoplasma* 154: 161–171.
- Stevenson, D. W. (1975). Taxonomic and morphological observations on *Botrychium multifidum* (Ophioglossaceae). *Madrono* 23: 198–204.
- Stevenson, D. W. (1980). Observations on root and stem contraction in cycads (Cycadales) with special reference to *Zamia pumila* L. *Bot. J. Linn. Soc.* 81: 275–281.
- Thoday, D. (1926). The contractile roots of *Oxalis incarnata*. *Ann. Bot. OS* 40: 571–583.
- Thoday, D. (1931). Mechanism of root contraction in *Brodiaea lactea*. *Pl. Physiol. Lancaster* 6, 721–725.
- Thoday, D., and Davey, A. J. (1932). Contractile roots. II. On the mechanism of root-contraction in *Oxalis incarnata*. *Ann. Bot. OS* 46: 993–1005.
- Troll, W. (1937–1943). *Vergleichende Morphologie der höheren Pflanzen*. 1. Vegetationsorgane. Borntraeger, Berlin.
- Watanabe, K. (1925). Über die Kontraktion und daraus verursachte Anomalie in der Wurzel von *Cycas revoluta*. *Jpn. J. Bot.* 2: 293–297.
- Wilson, K., and Anderson, G. J. H. (1979). Further observations on root contraction. *Ann. Bot. NS* 43: 665–679.
- Wilson, K., and Honey, J. N. (1966). Root contraction in *Hyacinthus orientalis*. *Ann. Bot. NS* 30: 47–61.
- Woodhead, T. W. (1904). Notes on the bluebell. *Naturalist* 566: 41–48, 81–88.
- Zamski, E., Ucko, U., and Koller, D. (1983). The mechanism of root contraction in *Gymnarrhena micrantha*, a desert plant. *New Phytol.* 95: 29–35.
- Zimmermann, M. H., Wardrop, A. B., and Tomlinson, P. B. (1968). Tension wood in aerial roots of *Ficus benjamina* L. *Wood. Sci. Technol.* 2: 95–104.

Plant Roots

The Hidden Half

Second Edition, Revised and Expanded

edited by

Yoav Waisel
Amram Eshel

Tel Aviv University
Tel Aviv, Israel

Uzi Kafkafi

Hebrew University of Jerusalem
Rehovot, Israel

Marcel Dekker, Inc.

New York • Basel • Hong Kong

Copyright © 1996 by Marcel Dekker, Inc.