UNDERGROUND PLANT MOVEMENT. V. CONTRACTILE ROOT TUBERS AND THEIR IMPORTANCE TO THE MOBILITY OF HEMEROCALLIS FULVA L. (HEMEROCALLIDACEAE)

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The ornamental daylily, *Hemerocallis fulva* (Hemerocallidaceae), possesses a short, vertically oriented basal shoot packed with a circle of root tubers that are exhausted during sprouting after dormancy. During the growth period a new circle of root tubers is formed, enabling the plant to survive the next resting phase. In shallow-planted individuals the new root circle appears just above the old one. The new root tubers show strong contractile activity and pull the cryptocorm downward. Deep-planted cryptocorns of *H. fulva* move upward by the growing shoot tip. During the spraying process, a few internodes of the deeply located shoot tip elongate, and thus the new root circle appears at a distance of several centimeters from the old root circle. However, this shoot elongation only appears when the individual is positioned very deeply in the soil (facultative shoot elongation). Induction experiments make clear that the parameters (light, temperature fluctuations) that normally influence the activity of contractile roots cannot regulate root contraction in *H. fulva*. Contraction is a base characteristic of *H. fulva* roots and always functions to pull down the vertical shoot. However, individuals of *H. fulva* are well adapted to secure the best soil position for survival by having two mechanisms to regulate soil depth: the pulling effect of contractile roots, and, as an emergency response, the opposite effect of upward growth of the facultative shoot elongation.

**Introduction**

Mobility of underground plant organs (e.g., bulb, corn; "cryptocorm" in Troll 1964) results from the activity of contractile roots. These movements can be observed directly and presented as time-lapse photographs (Pütz 1993, 1994, 1996b, 1996c). This phenomenon is important first, to secure an underground position, and second, to reach an ecologically useful position (Pütz 1996b).

Depth regulation in particular is only possible when a species is able to register its actual depth and respond, when necessary, e.g., by producing contractile activity of its roots (Rimbach 1897; Kirchner et al. 1934). However, little work has been done to classify the parameters responsible for registration of soil position. Inductive parameters are (1) illumination of the sheath leaves and/or (2) rapid diurnal temperature fluctuation in the soil. However, the effect and combination of these parameters varies from species to species (Galil 1958; Jacoby and Halevy 1970; Iziro and Hori 1983; Halevy 1986, Pütz 1996b; Pütz et al. 1997).

Our current knowledge is limited to species that develop "uniform roots" (that function for water and nutrition uptake and possibly for contraction, e.g., *Sauromatum, Narcissus,* or *Nothoscordum;* Pütz 1996b, 1996c) and, in contrast, to species that have nutrient roots and develop special contractile ones when pulling is necessary (Heterorhizie, "Zugwurzel," Rimbach 1898; "pulling root," Duncan 1925; e.g., *Gladiolus, Leopoldia,* or *Arisarum*). However, less is known in relation to underground movement for another group of monocotyledonous species. These species have roots that function for water uptake, contraction, and, additionally, storage for the next year's sprouting, which could be called "contractile root tubers" (*Hemerocallis fulva,* Arber 1925 and Pütz 1996a; *Agapanthus umbellatus,* Rimbach 1929; *Asphodelus cerasiferus,* Cauro 1968). The amount of pulling activity of contractile root tubers is very similar to uniform roots or to special pulling roots (Pütz 1992). Thus, it can be expected that contractile root tubers produce valuable underground movements of the cryptocorn. In *H. fulva* (Hemerocallidaceae), a well-known ornamental (daylilies), we found an ideal object for observing underground movement directly and for making experiments to identify the parameters that possibly induce a contractile effect in root tubers.

**Material and Methods**

A morphological description of *Hemerocallis fulva* L. can be found in Kirchner et al. 1934 (pp. 317-321) and Dahlgren et al. 1985 ("Lily-like, glabrous herbs to ca. 1 m tall with short rhizomes and fleshy, swollen, sometimes nearly fusiform roots. The larger leaves are concentrated at the base" [po 177]).

During the resting phase in winter, adult plants were selected from the Botanical Garden of Aachen. These plants have short, vertical basal shoots (Grundachse) packed with root tubers.1

**Direct Observation of the Underground Movement**

Thirty individuals of *H. fulva* were planted shallowly (1 cm below the soil surface) in special test containers and cultivated in the greenhouse of the Botanical Institute of the Rheinisch-Westfälische Technische Hochschule Aachen at a minimum temperature ranging from 14°C at night to 25°C during the day (up to 35°C on sunny days). Plants were illuminated for 12 h daily using plant lamps (Osram, Power Star HQI-T-400 W/DH, Frankfurt, Germany). Plants were dug out from one side and photographed at regular intervals (4 wk). A detailed description of the cultivation parameters, the test containers, and the preparation method are reported by Pütz (1993). Time-lapse

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1 According to Troll (1943), rhizomes store for sprouting in the next growth period. However, as he pointed out, the main function of short basal shoots, e.g., *Hemerocallis,* *Asphodelus,* or *Dahlia* is not to store. These short axes bear only the innovation buds, which sprout after dormancy. Storage is limited to the root tubers.
photography of some of the individuals was prepared. When planting the individuals, an aluminium control mark was located a few cm from the corn. The distance from the plant body to this control mark reflects its underground movement. In the time-lapse photography the control marks appear as white lines.

Another 30 individuals of *H. fulva* were observed in large test containers made of PVC (40 X 40 X 20 cm) with one removable side wall, attached to the container using clamps (Pütz 1994). The containers were filled with sieved sand/loam mixture, and in each of them, three individuals were planted at a depth of 25 cm below the soil surface. Observations were made every 4 wk. The side wall of the container was removed and the cryptocorms were carefully exposed, cleaned, and photographed as reported by Pütz (1993, 1994).

**Induction Experiments**

Thirty-two individuals of *H. fulva* of equal size (length of the basal shoot 40-50 mm, 15-20 root tubers) were pretreated under defined conditions of temperature and light. Half the individuals were cultivated (pot culture) in a greenhouse where rapid temperature fluctuations of $10^\circ-20^\circ$C between day and night occur (see above). The others were cultivated (pot culture) in a phytotron at a constant temperature ($20^\circ$C). In the greenhouse, and also in the phytotron, half the individuals were planted ca. 10 mm under the surface. The remaining individuals in each culture room were cultivated by simulating a deep soil position. This was achieved using a tube of dark-colored PVC (75 mm diam) through which the individual had to grow during sprouting. The tube was resting on the soil surface and was filled with small black beads of foam rubber. The length of the tube was 200 mm. After the growth period, four classes of pretreated individuals were available. These classes are identified by the following code system (according to Pütz et al. 1997; lowercase "t" and "T" symbolize pretreatment conditions): 1+/T15: with light on the sheath leaves, diurnal temperature fluctuations of $10^\circ-20^\circ$C; 1-20/t15: no light on the sheath leaves over a length of 200 mm, diurnal temperature fluctuations of $10^\circ-20^\circ$C; 1+/t0: with light on the sheath leaves, no diurnal temperature fluctuations; and 1-20/t0: no light on the sheath leaves over a length of 200 mm, no temperature fluctuations.

Four equally sized individuals from each pretreated class were chosen and were cultivated without soil in a mist culture chamber during the subsequent growth period (treatment, Pütz et al. 1997). Eight of these chambers were located in the greenhouse (temperature fluctuations), and another eight chambers remained in the phytotron at a constant temperature of $20^\circ$C ($\pm 1^\circ$C). The lower parts (200 mm) of half of all the plants were protected from illumination using PVC tubes as described above. The remainder reached light after 10 mm. Thus, during sprouting after dormancy, all leaves became illuminated. After the growth period, four classes of treated individuals were available (capital letters in the code system now stand for conditions during mist culture): L+/T15: with light on the sheath leaves, diurnal temperature fluctuations of $10^\circ-20^\circ$C; L-20/T15: no light on the sheath leaves over a length of 200 mm, diurnal temperature fluctuations of $10^\circ-20^\circ$C; L+/t0: with light on the sheath leaves, no temperature fluctuations; L-20/t0: no light on the sheath leaves over a length of 200 mm, no temperature fluctuations. However, planting was carried out to ensure a uniform distribution of the four classes of pretreated individuals in the culture chambers, i.e., individuals of each class of pretreatment were treated by L+/t0, L+/T15, L-20/t0, and L-20/T15. Thus, we included all possible combinations of pretreatment and treatment (see Pütz et al. 1997).

**Second Repetition of Induction Experiments (Dark Experiments)**

The whole procedure of pretreatment and treatment was repeated with new individuals of equal size (see above). However, this time during treatment all plants were protected from illumination using PVC tubes. In the greenhouse each of two individuals was covered over a length of 200 mm (L-20), 300 mm (L-30), 500 mm (L-50), and 700 mm (L-70). The same procedure was used with the individuals fixed in the mist culture chambers in the phytotron.

**Dry Weight**

The dry weight of the tested plants was determined by drying an individual at 105°C. This was deemed necessary to make sure that the overall vitality of all individuals was the same.

**Measurements**

In the mist culture chambers, root activity was measured using the lifting technique (Pütz 1992). Roots were introduced into small plastic tubes filled with substratum (mass = 75 :!: 5 g). The degree of contraction was determined by measuring the change in distance between the tube and the surface of the support during the experiment (Pütz 1992; Pütz et al. 1997). To establish the individual in the mist culture, the first five roots were not measured. Measurements were carried out on successive root tubers. In the culture chambers, space was limited, and it was therefore only possible to measure a maximum of 11 roots for each individual.$^2$

Over a time span of 3 yr, 261 roots from 32 individuals have been measured.

**Calculations**

The pulling force (in N) of a single contractile root can be calculated by multiplying tube mass by acceleration. Since acceleration is a constant, increasing tube mass results in an increase in pulling force. However, as Pütz (1992) has shown for *Sauromatum guttatum*, an increase in tube mass results in a decrease in lifting movement, and the magnitude of variation of the values of work remains small, indicating that work is the most useful way to compare the root activity of various individuals. Work (1) can be calculated by the distance of tube movement multiplied by the calculated force. Maximum work is defined as the work a single root is able to carry out until contraction has been completed (Pütz 1992). A calculation is made to determine the average maximum work of each individual tested. Moreover, to determine the significance of the various parameters involved in contractile root activity, the average maximum work values of some “groups of plants” were calculated. The calculations of these groups of plants include the single root measurements of all individuals having a defined parameter. Calculation for each parameter divides the total of 261 single root measurements into two groups,

$^2$ Old root tubers of *Hemerocallis fulva* from the previous growth period have no contractile activity (cf. Pütz 1992 for *Asphodeles aestivus*).
e.g., light pretreatment: 1+ (average of 126 measurements) and 1-20 (n = 135); temperature treatment: TO (n = 117) and T15 (n = 144); temperatur...easurements not only into two groups with respect to light treatment (L+, L-) but into five groups of plants: L+ (66 measurements), L-20 (n = 110), L-30 (n = 43), L-50 (n = 30), and L-70 (n = 12).

Results

Direct Observation of the Underground Movement

During the sprouting process the old root tubers of *Hemerocallis fulva* individuals were consumed. Shallow-planted individuals formed a rosette of leaves at the top of the short vertical stem. In their underground parts, the individuals developed a circle of new roots on the vertical stem, just above the old ones (fig. 1A, B). The new roots have a strong ability to contract, which is ultimately recognizable by the wrinkled surface of their proximal root parts. As a result, the whole plant moves downward (fig. 1). The distance from the bottom of the rosette to the control line is a benchmark for the quantity of the downward movement. The individual (fig. 1) reaches a 50 mm deeper position during a time span of 8 mo. However, this moving distance varies from 12 to 65 mm in the 30 tested individuals, with an average 35.0 ±: 15.2 mm. The older, exhausted roots (fig. 1C, D) show a secondary change of their course caused by continuous movement.

However, deep-planted individuals of *H. fulva* react very differently. During sprouting, the basal shoot does not remain short, as it appears in shallow-planted individuals, but elongates (fig. 2A). The elongated axis has small pale scale leaves and consists of only four to six internodes (figs. 2B; 3). When the upper scale leaf (scale leaf 6 in fig. 3) becomes exposed to light, shoot elongation stops. The apical meristem of the stern now produces foliage leaves instead of scale leaves. The internodes remain short, and thus the foliage leaves form a rosette a few centimeters below the soil surface. The new root tubers are formed adventitiously from the axis, mainly from the internodes of the first foliage leaves (internodes 8-10 in fig. 3B).

The circle of new root tubers is at a large distance from the old circle of root tubers (fig. 2B), and the distance from old to new root circle in the individuals tested ranges from 70 to 210 mm, with an average of 147 ±: 40 mm. The new roots shorten and pull the leaf rosette downward. In 5 wk (cf. fig. 2B, C), the rosette has increased its distance to the soil surface from 55 to 65 mm, i.e., the distance to the control line changed from 35 to 45 mm. As a result of this downward movement, the elongated shoot bends or buckles (arrows in figs. 2, 4). However, the distance moved downward during one growth period is not of the same magnitude as in shallow plants and ranges only from 6 to 23 mm (average of all tested individuals: 14.6 ±: 4.8 mm).

Furthermore, when dug out completely, most of the new root tubers have local swellings in their distal parts (figs. 2, 4) containing stored food (starch) for sprouting after dormancy.

In both shallow- or deep-planted individuals, vegetative spreading of ramets appears. These runners develop from axillary buds of the scale leaves and remain short in shallow plants (10-50 mm). However, in deep positioned plants, the runners elongate up to 480 mm, limited in our experiments by the wall of the test container.

In many of the tested deep-oriented plants, runners appear. The runners were first oriented horizontally (plagiotropically) for at least 160 mm, but then turn to the vertical direction (fig. 4). Finally, the runners reach light and then develop a rosette of leaves and root tubers and separate from the mother plant by an interruption of the connection at the base of the ramet.
Induction Experiments

While the condition of the tested plants of the first experiment appeared to be very good, some dark...
Discussion

Underground movement is an ecologically important phenomenon in accomplishing at least three functions (Pütz 1996a): (1) achieving an appropriate soil position, particularly as occurs with seedlings (e.g., *Arum maculatum*, Rimbach 1898; *Chlorogalum pomeridianum*, Jernstedt 1984; direct observation, e.g., for *Lapeirousia laxa* and *Foeniculum vulgare*, Pütz and Sukkau 1995); (2) vegetative spreading of ramets (daughter corms or bulbs) by the activity of contractile roots may be quantitatively small (only a few millimeters, e.g., *Nothoscordum inodorum*, Pütz 1993). In some species, however, it can reach 10-50 cm (e.g., *Triteleia hyacinthina*, Smith 1930; *Allium neapolitanum*, Galil 1965; *Oxalis pes-caprae*, Galil 1968 and Pütz 1994); (3) securing a safe position in the soil to survive cold winters or dry summers is important especially for geophytes. In earlier investigations depth regulation has been assumed, based on the position of the plant body (e.g., Rimbach 1898; Arber 1925; Galil 1980). To date this “securing movement” has been shown directly for bulbs (*Nothoscordum inodorum*, Pütz 1993; *Narcissus tazetta*, *Galtonia candicans*, Pütz 1996c) and corms (*Sauromatum gutatum*, *Arum italicum*, *Arisarum vulgare*, Pütz 1996b).

In horizontally oriented rhizomes, which are common in many plant species, securing an appropriate position in the soil is generally achieved by the growing activity of its shoot tip (Rimbach 1899; Arber 1925; Galil1980), which, as necessary, is able to grow up or down (Rimbach 1899; *Polygonatum* spec., Raunkiaer 1934; *Aegopodium podagraria*, Bennet-Clark and Ball 1951). In vertically oriented cryptocorms, however, appropriate soil position is achieved either by the activity of contractile roots alone, e.g., the downward movement of bulbs (Pütz 1993, 1996c), or contractile root activity is combined with corm growth, e.g., downward movement of vertical corms (Pütz 1996a, 1996b).

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**Fig. 3 Hemerocallis luiva.** A, Line drawing of a deep-planted individual 6 wk after sprouting. B, Schematic outline to show succession of internodes and leaves (ascending order is indicated by numbers). Bars represent 10 mm. **Ra**, rosette; **CR**, contractile root (**O**, old root tubers from the last growth period; **n**, new roots); **Fl**, foliage leaves; **In**, internode; **Sh**, shrinkage of root surface; **Si**, scale leaf; **Sis**, scale leaf scar; **Sw**, local swellings.
In relation to shallow-planted individuals of *Hemerocallis fulva*, the situation is very similar to vertical corm movement. The growing activity of the shoot is upward, but the internodes remain very short, and thus upward movement by shoot growth is very small (in the tested individuals ca. 5-10 mm). In contrast to this ascension, downward movement of the shallow-planted cryptocorms occurs much more because of the pulling activity of the new root tubers. Kirchner et al. (1934, p. 319) distinguish different root types in *H. fulva*: “Die der Grundachse angehörigen Wurzelfasern sind bei *Hemerocallis fulva* entweder zylindrisch und teils glatt, teils runzelig, oder sie haben eine knollig.

Fig. 4 *Hemerocallis fulva*. View of three deep-planted individuals, using time-lapse photography to show the total underground movement including (1) upward movement as a result of shoot elongation, (2) downward movement by root contraction, and (3) vegetative spreading by a runner. Date of examination is given in the lower section of each photo. Bars represent 50 mm. CR, contractile root (O, old root tubers from the last growth period; n, new roots); EL, elongation of the axis; Ru, rosette; RU, runner; S1, scale leaf; Sw, local swellings. The arrows show the bending of the elongated axis caused by continuous pulling of the new roOIS.
Gradients of chemical compounds in the soil may be responsible for recording depth in that the presence of 5% CO₂ made rhizomes grow upwards. High concentration of special chemical compounds could also relate to this topic.

Some species are able to register their soil depth and react either by forming no more contractile roots (Galil 1958; Halevy 1986; Pütz 1996b; Pütz et al. 1997), or by changing the contractile root properties (Rimbach 1897, 1898). In contrast to this, our lifting measurements make clear that in H. fulva the activity of the root tubers is independent of temperature fluctuations and illumination. These results contrast with all experiments about root induction so far carried out. Except for the very first roots at the beginning of the sprouting process, which were not measured in our experiments, all new root tubers of the mist culture plants produce a comparable root force and work. Furthermore, in the deep-planted H. fulva individuals of the pot culture experiments, the root tubers of the new root circle still have the ability to pull and thus bend the elongated axis. Overall, it seems useful to assume that H. fulva is not able to regulate its contractile activity to any degree.

Hemerocallis fulva individuals record their soil depth and react very quickly in a surprising and remarkable way but one that does not involve root contraction. In the first phase of sprouting, the deeply rooted individuals seem to register their depth and, in response, elongate their axes to several centimeters. However, in contrast to many rhizomatous plants, which regularly develop elongated phases between their thickened parts (e.g., Arber 1925; Troll 1943; Holturn 1955; Bell 1994), shoot elongation in H. fulva occurs only at very deep soil positions. At normal soil depths the vertical shoot remains short. This "facultative shoot elongation" is known in principle for other species, e.g., the bulbs of Leucojum vernum and Galanthus nivalis (Kirchner et al. 1934) or the corm of Crocosmia x crocosmiiflora (Bell 1994). This phenomenon is an immediate and quick response to unfavorable soil conditions and has the opposite effect to the downward movement of root contraction, thus making regulation of root contraction redundant.

The parameters responsible for shoot elongation are unknown. It might be expected that a lack of illumination and/or temperature fluctuations are marks for the plant to record a deep soil position. However, our induction experiments show that all tested plants in the mist culture system still have short vertical shoots and develop the new root circle just above the old one. This means that light and temperature, which are responsible for root contraction in other species, have no effect in H. fulva, neither for contractile activity nor for shoot elongation. There are so many other possible parameters that could be used by plants in detecting their depth. Examples are soil gradients of chemical compounds, e.g., a decrease of Oz or an increase of CO₂ in deeper soil layers. The only experimental approach known on this topic relates to the upward movement of rhizomes of Aegopodium podagraria. Bennett-Clark and Ball (1951) report that the presence of 5% CO₂ made rhizomes grow upward. High concentration of special chemical compounds could also clarify why shoot elongation appears in pot culture experiments, but not in deeply rooted individuals in mist culture. Gradients of chemical compounds in the soil may be responsible for recording depth in H. fulva, and future work will deal with this topic.

Table 1  Average of Dry Weight (in g) of the Tested Individuals, Which Were Exposed to Different Levels of Light Illumination

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<th>L+ (Line)</th>
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<th>L-20 (2 dex.)</th>
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<td>66 ± 10</td>
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<td>64 ± 18</td>
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Note. Light illumination (L+, L-20, L-30, L-50, L-70): n, number of individuals; Line, plants from the first induction experiments; 2 dex., plants from the dark experiments.

Fig. 5 Hemerocallis fulva. Average maximum work (in Joules) and standard deviations for different group of plants of defined parameter. Pretreatment completed in the previous growth period: light L+ (with light on the sheath leaves) and light L-20 (no light on the sheath leaves over a length of 200 mm); T0 (no diurnal temperature fluctuations) and temperature t15 (diurnal temperature fluctuations). Treatment (done in the subsequent growth period): TO without diurnal temperature fluctuations, T15 (with diurnal temperature fluctuations), L+ (with light on the sheath leaves), L-20 (no light on sheath leaves over a length of 200 mm). L-30 (no light on sheath leaves over a length of 300 mm), L-50 (darkening of 500 mm), L-70 (darkening of 700 mm). Numbers in the last line show the number of single root measurements involved in the calculation for each column.
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