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The Induction of Contractile Root Activity in *Sauromatum guttatum* (Araceae)

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Abstract: (contraction of *Sauromatum guttatum* roots creates a slow, downward underground corm movement, the corm becoming covered by a greater amount of soil, and the geophilous plant surviving the dormancy period at a safer soil position. (orm movement of *Sauromatum guttatum* is only possible if root contraction results in pulling activity. This pulling activity can be quantified using the lifting technique. Measurements of the pulling activity are shown as working curves over time and as the maximum work of a single contractile root. Our results show that root activity varies in individuals cultivated under different parameter conditions. It can be shown that two factors induce root contraction: first, rapid temperature fluctuations during the preceding growth period; second, illumination of the sheath leaves during the actual growth period. However, light induction is, as found here, more important and hierarchically superior, for the temperature effect is only seen in plants whose sheath leaves are not illuminated. Mobility of *S. guttatum* plants can thus be described as photo-movement. If the light effect is not present, the mobility of *S. guttatum* may become thermo-movement. However, at present, there is no indication that this movement is oriented to the direction of stimulus.

Key words: *Sauromatum*, root contraction, induction, movement.

Abbreviations:

I- pre-treatment, no light on the sheath leaves

I+ pre-treatment, with light on the sheath leaves

T15 pre-treatment, day/night temperature fluctuations of
10-20°C

TO pre-treatment, no temperature fluctuations

L- treatment, no light on the sheath leaves

L+ treatment, with light on the sheath leaves

T15 treatment, day/night temperature fluctuations of 10-20°C (TO treatment, no temperature fluctuations)

Introduction

As we have shown in time lapse pictures (Pütz, 1993,1994,1996), the function of contractile root activity in general is to move an underground plant body, e.g. to reach and retain a safe position in the soil. In deeper soil positions, soil conditions (e.g. water, temperature) are closer to average and plant organs are less likely to be subjected to drying or freezing during the dormancy period. If the plant body is positioned at greater soil depths, contractile root activity may decrease, e.g. some species develop no contractile roots at all (Galil, 1958; Halevy, 1986), while in the case of others, contractile root properties change (Rimbach, 1897,1898,1899). Thus, it would appear that at least some species are able to record their soil depth, responding with a change in contractile root activity, and, as the final consequence, changing the moving response of the plant body.

The first person to carry out experiments relating to this topic was Galil (1958). He pointed out that, in *Leopoldia maritima*, rapid temperature fluctuations of the soil were responsible for the formation of contractile roots. Iziro and Hori (1983) reported further details about temperature promoting contractile roots in *Gladiolus spec.* and *Oxalis bowieana*. Finally, Jacoby and Halevy (1971) and Halevy (1986) have examined individuals of *Gladiolus* and identified two parameters as being responsible for the induction of contractile root formation: light illumination on the upper sheath leaves, and temperature fluctuations in the root initiation zone.

The species investigated develop two kinds of roots, small nutrient roots and bigger contractile ones, showing (1) an increase in root thickness and (2) a shrinkage of the root surface as the most visible signs of root contraction. In these cases, it seems possible to count the number of contractile roots of individuals planted under different conditions, and to draw some conclusions about contractile root formation in relation to such parameters as light or temperature.

Most species having root contraction do not form special contractile roots, but show only one kind of root, whose function is nutrition and contraction (e.g., Alliaceae, Amaryllidaceae, Araceae), and, in some cases, even storage (e.g., Hemerocallidaceae). Thus, analysis of pulling activity by counting the number of contractile roots is impossible. In *Nardus tazetta* (Amaryllidaceae) and *Nothoscordum inodorum* (Alliaceae), we were able to take the macroscopic features of contraction (swelling and shrinkage) as a benchmark for pulling activity (Pütz, 1996a). In these species, illumination of the basal leaf parts is the only parameter thus far identified as regulating root contraction and bulb movement.

However, in preliminary pot culture experiments with *Sauromatum guttatum* Schott it became clear that neither swelling nor shrinkage were distinctive signs of the pulling activity in this species. Therefore, individuals of *S. guttatum* were grown in a mist culture system under various cultivation conditions. We measured the pulling activity of single contractile roots using the lifting method (Pütz, 1992).

Expressed in force, work or power, these measurements provided quantitative factors useful for comparison, and in discovering which parameters induce root contraction and corm movement.

Materials and Methods

During the resting phase in winter, corms of *Sauromatum guttatum* Schott. (Araceae) of equal size (50-60mm diameter) were selected at the Botanical Garden of the R. W. T. H. Aachen. A detailed description of growth and movement of *S. guttatum* is given in Pütz (1996). Sprouting of the corm occurs after a resting phase of about six months and takes place in darkness. The corm first develops three scale leaves (sheath leaves) and 1 - 3 foliage leaves, which form a leaf stem (Figure 1). After the first foliage leaf unfolds, the sheath leaves degenerate. The roots appear successively at the top of the corm and function for nutrition and contraction. During the growth season the old corm becomes exhausted and the new corm develops just above (vertical corm).

Pre-treatment

The individuals were cultivated in planting containers (5 litres), filled with riddled sand/loam mixture. Half the individuals were cultivated in a greenhouse with minimum temperature ranging from 14°C at night to 25°C during the day (on hot summer days the maximum temperature measured was up to 35 °C, even in the shade). The other corms were cultivated in a phytotron at a constant temperature of 20°C (+/- 1°C). The plants were illuminated for 12 h daily using plant lamps (Osram, Power Star HQI-T 400 W/DH).

In the greenhouse, and also in the phytotron, half the individuals were planted approx. 10 mm under the soil surface. Thus, during sprouting all leaves became illuminated, the sheath leaves as well as the foliage leaves (Figure 1 A). The remaining individuals in each culture room were cultivated by simulating a deep soil position. This was achieved using a tube of dark pvc (60 mm diameter), 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, and thus the first 180 mm of the leaves were shielded from any illumination. This depth ensures that only the tips (and no other parts) of the sheath leaves will be illuminated. After the vegetation period, four classes of pretreated individuals were available:

I+/t15 = light on the sheath leaves, temperature fluctuations (greenhouse)

I-/t15 = no light on the sheath leaves, temperature fluctuations (greenhouse)

I+/t0 = light on the sheath leaves, no temperature fluctuation (phytotron)

I-/t0 = no light on the sheath leaves, no temperature fluctuation (phytotron)

Treatment

During the following growing period, 16 pre-treated individuals of equal size (50 - 60 mm diameter) were cultivated without soil in a mist culture system. The corm was placed on a stand (see Figure 1 B), fixed in place with coated wire and put into a culture chamber, where the plants were sprayed with Knop's nutrient solution for 15 s at hourly intervals (for a detailed description see Pütz, 1992). Eight of these chambers were located in the greenhouse (temperature fluctuations, T15), another eight chambers remained in the phytotron (T0) at a constant temperature of 20°C (+/- 1°C). The lower parts (180 mm) of half of all plants were protected from illumination

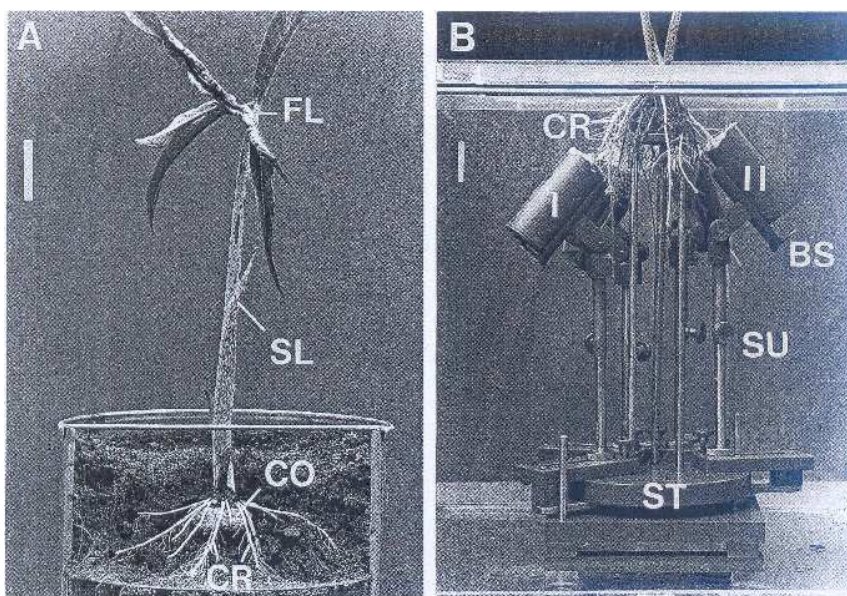


Fig.1 *Sauromatum guttatum*, A) Entire plant in pot culture, the underground parts have been dug out; B) View inside a culture chamber. The distance of tube I to the bearing surface demonstrates the pulling activity of the root. I, II different tubes; ST stand; BS bearing surface; SU support; CO corm; CR contractile root; SL sheath leaf; FL foliage leaf. Bars represent 30 mm.

tion using PVC tubes as described above (L-), the others were planted approx. 10 mm under the soil surface, thus, during sprouting, all leaves became illuminated (L+).

After the vegetation period, for classes of treated individuals were available: L+/T15; L+/TO; L-/T15 and L-/TO. However, planting was carried out to ensure a uniform distribution of the four classes of pre-treated individuals in the culture chambers, e.g. individuals of L+/TO were treated by L+/TO, L+/T15, L-/TO and L-/T15 etc. Thus, with four pre-treated classes and four classes of treatment, a total of 16 individuals of different parameter combination were available at the end of the second growth period (e.g. L+/TO/L+/TO; L+/TO/L+/T15; L+/TO/L-/TO; etc.).

The whole procedure of pre-treatment and treatment was repeated, i.e. over a time span of three years a total of 32 individuals were examined to quantify the activity of single contractile roots in relation to various parameters.

Measurement

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 of 75 ± 5 g) and fixed with a packing ring made of plaster of Paris (Pütz, 1992). The extent of contraction was determined by measuring the change in distance between the tube and the surface of the support during the course of the experiment. In Figure 1 H, two measurements can be seen. Tube I is resting on the bearing surface of the support (beginning of an experiment), Tube II being lifted off by root pulling. This tube lifting was measured at intervals of two days and lasted approx. 45 days for a single contractile root. To establish the individual in the mist culture, the first 10 roots were not measured. For the following roots, measurements were carried out. In the culture chambers, space is limited, and it was therefore only possible to measure 5 - 7 roots of each individual.

Calculation

The pulling force (in N) was calculated by multiplying tube mass by acceleration. 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 the lifting movement, and the magnitude of variation of the values of work remains small. This means that the value of work is most useful in comparing the root activity of various individuals. To determine the work (in J) of a pulling root, the distance of tube movement is multiplied by the calculated force. Work was calculated for each tube lifting step measured, and thus a curve is available for increase of work relative to time, finally reaching the maximum work. For each parameter combination (pre-treatment and treatment, e.g. L+/TO/L+/TO, etc.), an average curve for increase of work over time was made (each from 10 - 11 single root measurements of two individuals).

Additionally, calculation of the average maximum work was carried out. This seems to be necessary in detecting the significance of the various parameters involved in contractile root activity. Calculations were made by 'group of plants', including all individuals having a defined parameter: L+

(average of 87 root measurements of 16 individuals), L- (average of 87 root measurements of 16 individuals), T15 (87/16), TO (87/16), L+/T15 (87/16), L+/TO (87/16), L-/T15 (87/16), L-/TO (87/16). In addition, similar calculations were made for plants without light treatment (L-), in combination with another parameter: L-/TO (43/8), L-/T15 (44/8), L-/L+/T15 (43/8), L-/L+/TO (44/8), L-/L-/T15 (44/8), and L-/L-/TO (43/8).

Results

The pulling activity of a single contractile root can be shown in curves of increase in work in relation to time (Figure 2). We have found three types of curves, which differ significantly. In curves of type A, the pulling work of the root increases, and eventually reaches a plateau at a level of at least 0.32 J. Table 1 shows the average maximum work of the roots of all plants with different parameter combinations, thus, e.g. the individuals in Figure 2A, [L+/T15 L-/TO L+/I], have contractile roots which build up to a work level of 0.39 J (average of 10-11 measurements). Table 1 shows that this type of curve occurs in plants of different parameter combinations and can be found eight-times among the individuals having a treatment of light (L+).

In curves of type B, the pulling work increases, but eventually reaches a plateau at a lower level. The individuals in Figure 2 H, [L+/T15 L-/TO L-], show an average contractile root activity of only 0.12 J (Table 1). This type occurs four-times in Table 1,

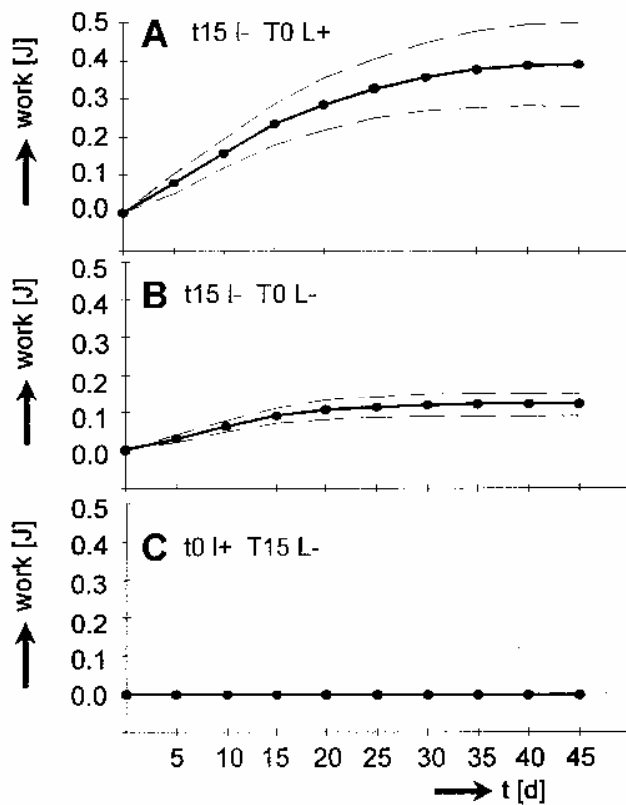


Fig.2 Measurement of root activity (working curves) of plants with various parameter combinations (A, B, C, each curve representing the average of 10-11 single root measurements). The dotted lines indicate standard deviation and show a significant difference in the total amount of work (W, in Joules).

Table 1 Maximum work (J) of a single contractile root of *Sauromatum guttatum* measured in each culture chamber (each value represents average and standard deviation of 10-11 single root measurements). Maximum work is represented by the various working curves (type A, B, C, see Fig. 2)

Culture chambers in the phytotron: Treatment T0							
	L+ t15 l+	L+ t15 l-	L+ t0 l+	L+ t0 l-	L- t15 l+	L- t15 l-	L- t0 l-
Type A	0.35 ± 0.07	0.39 ± 0.11	0.41 ± 0.05	0.37 ± 0.05			
Type B					0.14 ± 0.03	0.12 ± 0.03	
Type C							0.00 ± 0.00 0.00 ± 0.00
Culture chambers in the greenhouse: Treatment T15							
	L+ t15 l+	L+ t15 l-	L+ t0 l+	L+ t0 l-	L- t15 l+	L- t15 l-	L- t0 l-
Type A	0.33 ± 0.08	0.38 ± 0.07	0.33 ± 0.08	0.32 ± 0.08			
Type B					0.13 ± 0.02	0.14 ± 0.02	
Type C							0.00 ± 0.00 0.00 ± 0.00

and seems to appear only in some plants having a temperature pre-treatment. Curves of type C represent roots of plants having no pulling activity (e.g. [tO 1+ T15 L-] in Figure 2 C) and occur four-times in Table 1, distributed among the plants having had no temperature pre-treatment.

Calculation of average values and standard deviations from maximum work for "groups of plants" subjected to different parameters is useful in determining whether a particular factor is required in pulling activity. Taking all measurements into account, temperature treatment (TO versus T15), pretreatment of temperature (t15 versus tO) and light (1+ versus 1-) do not produce different contractile root activities (see hatched columns in Fig. 3), and thus, seem to have no inductive effect. The only parameter showing significant differences is light in the year of measurement (see Figure 3, treatment: L+: 0.36 :t 0.08J). However, even deep-planted individuals (without light treatment, L-) still show slight contractile root activity with an average work of approx. 0.06 :t 0.07 J. This activity of deep-planted individuals (L-) could be autonomous. However, the level of activity ranges from zero to 0.14J (compare Table 1) and thus points to another parameter inducing pulling activity, but which is superimposed by light treatment. To verify this, the calculation was repeated for "group of plants" having no light treatment (L-) in combination with another parameter. While treatment of temperature (L-{TO versus L-{T15) and pre-treatment of light (L-{1+ vs L-{1-) had no effect, splitting of L- plants into two groups of different temperature pre-treatment (L-{t15 versus L-{tO) results in a definitely different effect. L-individuals with temperature changes in the previous vegetation period (L-t15) show a contractile root activity of approx. 0.13 :t 0.03 J but those with no temperature changes in the preceding year

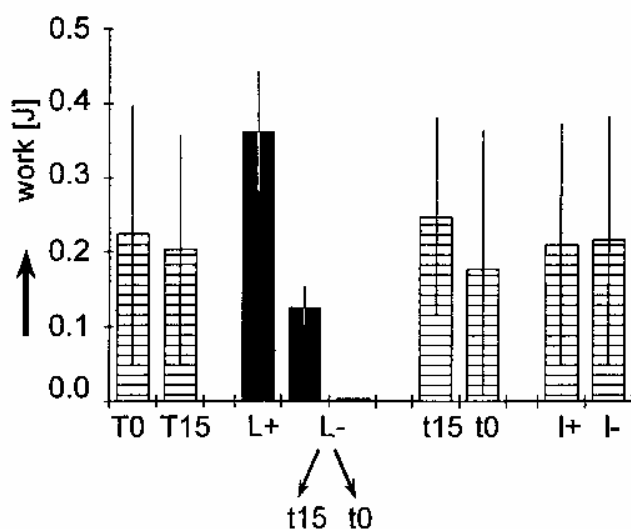


Fig.3 Average work and standard deviations for different "groups of plants" of defined parameter (treatment: light (L +, L-) or temperature TO, T15); pre-treatment: light (1+, 1-) or temperature (W, t15), for calculation see Materials and Methods). Each column represents the measurements of 16 plants and 87 single roots, with the exception of the "group of plants" having the treatment L-, which were divided according to their temperature pre-treatment, t15 and W. These two columns (L-{t15 and L-{W) show the average work of eight individuals with 43 -44 single root measurements. Black columns represent the parameters which produce a quantitatively measured induction effect.

(L-ta) have no contractile root activity (Figure 3). Thus, it would appear that day/night temperature changes of 10200(in the previous growing season have an inductive effect on the development of contractile roots in the following season. However, this temperature effect is significantly smaller than the light induction.

Maximum work, given in Table 1 for each parameter combination, is of the same order of magnitude in every case in relation to light treatment (L+). This indicates that the two parameters are not additive. Light induction alone leads to maximum contraction activity. A temperature effect is only detected when light is not acting.

Discussion

The experiments carried out to date make clear that two ecological parameters, illumination and soil temperature changes, are responsible for contractile root activity. There may exist other parameters of use to plants for detecting depth, e.g. water or chemical compounds (02, (02). However, these factors could only be useful if they conform to a gradient in the soil. With a mist culture there are no such gradients for *S. guttatum*. Halevy (1986) pointed out that corm size is another factor regulating the formation of contractile roots. He reports that *Gladiolus grandiflorus* plants with large corms do not form any contractile roots, but split into two or more daughter corms. Shallow-planted, large corms of *S. guttatum* (approx. 14-20 cm diameter) also branch into many corms (Pütz, 1996), but these still have contractile roots which bring about underground movement. Thus, planting large *S. guttatum* corms near to the soil surface does not affect the formation of contractile roots, but does affect corm growth and branching.

S. guttatum is a very good experimental subject, since it reacts to parameter changes by significantly different activities. Eight individuals do not show any contraction activity, and thus seem to demonstrate that there is no other parameter responsible for regulation of the activity of contractile roots. Visual features of root contraction, i.e. increasing root diameter and shrinkage, are not indicators of quantitative differences in contractile root activity in *S. guttatum* in relation to environmental conditions. For example, although we found a significant variation in activity using the lifting technique, roots of individuals showing either curve A or curve B (see Figure 2) look quite similar, both are 4–6 mm thick and show surface shrinkage proximally. Even roots of individuals with no activity (type C) are about 3–4 mm thick and show little surface shrinkage. Thus, our lifting-measurements are the only possibility of discovering the parameters which induce root contraction in *S. guttatum*.

Light-induction

Our culture chambers were covered with a wooden box (Pütz, 1992), so that only the upper parts of the plant could receive light. Halevy (1986), in *Gladiolus grandiflorus*, found the sheath leaves to be responsible for light reception. We found the same in *S. guttatum*. If *S. guttatum* corms are planted near the surface, most parts of the sheath leaves become illuminated during sprouting, even when the foliage leaves at their lower parts are covered. Planting *S. guttatum* corms at 15 cm or deeper below the soil surface means that only the tip of the upper sheath leaf will achieve exposure to light. Thus, illumination of the sheath leaves directly corresponds to the soil depth of the corm, and it appears that reception of light is localized in the upper sheath leaf. However, in *S. guttatum* these sheath leaves degenerate a few weeks after sprouting, and thus, an influence of photoperiodic changes seems improbable. However, we currently know nothing about the photoreceptor pigment. The only approach has been made by Halevy (1986) in discovering that red light was responsible for the treatment of *Gladiolus* contractile roots. However, his results are not specific enough for any conclusions to be drawn about the chemical components.

Perception of light produces a first response, the root contraction activity, which, as a second response, is responsible for underground corm movement (Pütz, 1992). This means that illumination is the external stimulus which eventually induces movement of the total organism (photo-movement). The only other example for such a photo-movement in higher plants could be the underground movement of growing rhizomes (Bennet-Clark and Ball, 1951; Raunkiaer, 1934; Mohr and Schopfer, 1994), but detailed investigations are lacking. Direction of movement in *S. guttatum* only depends on the direction of growth of the contractile roots, and in pot-cultured individuals we cannot find any influence of light on the direction of root growth in *S. guttatum*. Therefore, plant movement of *S. guttatum* by root contraction might be interpreted as a photophobic reaction.

Temperature induction

We have found no direct induction effect due to rapid temperature changes, as Galil (1958), Jacoby and Halevy (1970) and Halevy (1986) reported for *Leopoldia* and *Gladiolus*. However, in *S. guttatum*, temperature changes in the preceding vegetation period function as an induction for contractile root activity. At present, we know of no other example of such a thermophobic reaction in higher plants. Since quantification of root activity requires a great deal of work, we have not been able, so far, to localize where temperature reception takes place. However, Halevy (1986) has done some investigations with pot cultured corms of *Gladiolus* and found "that temperature treatment is perceived at the root-initiation zone". This also may be true of *S. guttatum*, although, in this species, information has to be stored during the resting phase, possibly in the root tips of the very young root buds. These root buds will grow out in the next vegetation period, retaining the information to be contractile. This might support the main function of contractile root activity in adult *Sauromatum* corms, which is to keep a safe soil position (Pütz, 1996). Temperature fluctuations seem to be a kind of "early warning" for the system to move deeper into the soil as a long-term response. Light illumination on the sheath leaf during sprouting is inducing an emergency response to move deeper more quickly.

Outlook

In summary, induction of contractile roots and/or contractile root activity occurs through various parameter combinations: temperature change (*Leopoldia maritima*, Galil, 1958), temperature change and illumination of the sheath leaves (*Gladiolus grandiflorus*, Halevy, 1986), illumination of the sheath leaves (*Narcissus tazetta*, *Nothoscordum inodorum*, Pütz, 1996a), or illumination of sheath leaves and temperature changes in the preceding year (*Sauromatum guttatum*).

Root contraction and the resulting plant movement play an important role in plant survival of geophytes and other lifeforms (Raunkiaer, 1934), especially if we remember that root contraction seems to occur in seedlings of many plant species (compare Pütz and Sukkau, 1995). Further investigations of contractile root induction are needed in relation to the reception (and storage) of the external stimulus. Furthermore it seems helpful to illuminate local parts of plants growing in the dark (compare Franzen et al., 1990) to get an idea of leaf-root communication. Furthermore, it will be necessary to know which anatomical changes occur during root contraction. Although there have been many examinations (e.g. Ruzin, 1979; Wilson and Anderson, 1979; Jemstedt, 1984), the anatomical mechanism of root contraction remains unclear (Pütz and Fraebe, 1995).

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