Cost and Advantage of Soil Channel Formation by Contractile Roots in Successful Plant Movement

NORBERT PÜTZ, GABRIELE HÜNING and HANS A. FROEBE

Botanisches Institut der R.W.T.H. Aachen, D-52056 Aachen, Germany

In most cases, contractile roots not only produce a pulling force on an underground plant (bulb, corm), but also push away the substratum and create a soil channel in which plant movement is made easier. Two specially-constructed experimental set-ups allowed the pulling and pushing activity of contractile roots in underground plant movement to be measured under identical standard conditions. Our results show that root channel formation is always advantageous for the accomplishment of movement. The extent of channel formation in relation to the size of the bulb or corm being moved was calculated as a percentage channel effect. A value of 100% indicates a channel effect sufficient to allow plant movement with no resistance. For smaller distances moved (20–30 mm) a small channel effect (10–40%) was found to be very efficient. For more extensive movement (> 50 mm) a 100% channel effect seems to be the optimum energetically. These systems of movement commonly exist in nature.

INTRODUCTION

Many underground organs such as bulbs or corms show underground movement (compare, e.g. Rimbach, 1898; Arber, 1925; Troll, 1937–1943; Galil, 1980; Pütz, 1993). On the one hand, the function of this movement is to regulate the depth of the plant, so that the individual can survive unfavourable seasons protected by an adequate amount of soil cover. On the other hand, lateral buds (daughter bulbs or corms) can be separated from the mother plant, so that vegetative spreading is possible (Smith, 1930; Galil, 1968; Pütz, 1994). In many cases this movement is effected by special roots, which build up a pulling force acting on the plant body. If the soil resistance is overcome, movement occurs. According to Rimbach (1898) and Froebe and Pütz (1988), the degree of movement depends on several parameters, including the form, size and surface of the plant body, as well as conditions of the substratum, e.g. soil type, moisture and density. The distance moved by the plant is, in most cases, only a few centimetres (e.g. *Nothoscordum inodorum*, Alliaceae, Pütz, 1993). However, some species show movement of 20 cm and above in the course of a single vegetation period (e.g. *Oxalis pes-caprae*, Pütz, 1994).

In most cases, the contractile roots or pull-roots (Rimbach, 1895; Duncan, 1925) lie in the pathway of the plant body and thus change the soil properties, according to the diameter attained by the root. Thickening of the root results in the soil beneath the plant body being pushed laterally. During root contraction, a soil cavity appears, equal in size to the root diameter. It is through this cavity that the plant body can be transported with only a small expenditure of energy, so that movement becomes much facilitated (Galil, 1978, 1980). Froebe and Pütz (1988)

showed that these cavities vary according to species, and describe this property of the contractile root as their channel effect (CE). According to Pütz (1992*a*), this effect can be calculated by the formula:

$$CE = \frac{Ar \times Nr}{Ao \times 2} \tag{1}$$

where Ar is the cross-sectional area of the pulling root, Ao is the maximum cross-sectional area of the bulb, and Nr the number of contractile roots. According to Pütz (1992*a*), it is reasonable to assume that half of all roots (Nr/2) are participating in channel formation during the pulling phase.

A root with a 100% channel effect (Fig. 1) forms a channel in which the plant body can be moved without any soil resistance (channel roots, z.B. *Triteleia hyacinthina*, Pütz, 1992*a*, *Oxalis pes-caprae*, Pütz, 1994). In many species a channel effect occurs that is normally less than 100%. In these cases, movement is easier (Pütz, 1992*b*), because soil resistance acts only on those parts of the plant body where there are no contractile roots (Fig. 1).

Therefore, in general, the **moving work** of contractile roots consists of (*a*) **pulling work** needed to overcome soil resistance, and (*b*) **radial expansion (pushing work)** needed to displace soil to form a channel (Fig. 1). Unfortunately, from an energetic point of view nothing is known about cost–advantage relationships in soil channel building. Therefore, we must ask whether it is energetically efficient for an individual to create a large channel. With the help of two new experimental set-ups we have obtained approximate values for both the pulling and pushing force, measured under identical soil conditions. Moreover, direct comparison of these results is useful in obtaining a cost–advantage
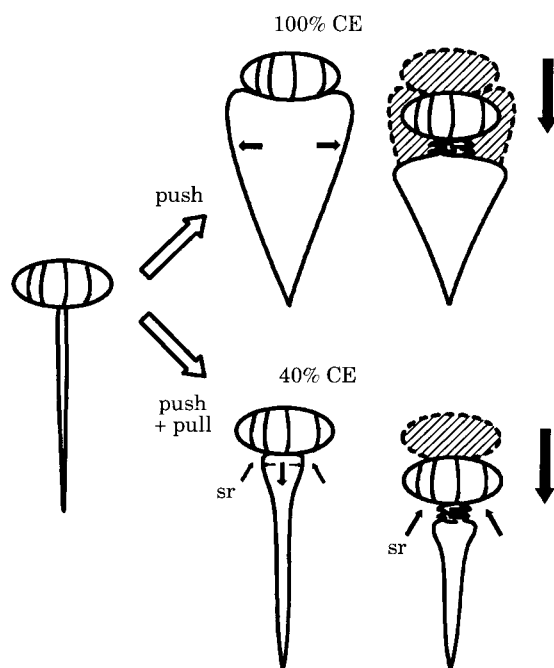
100% CE

push

push
+ pull

40% CE

sr

sr

FIG. 1. Diagram showing how underground plant movement depends on a pulling force and on a channel effect. The hatched area represents the starting position. The arrows symbolize the different forces: downward pulling, sideward pushing and the soil resistance (sr); CE, channel effect.
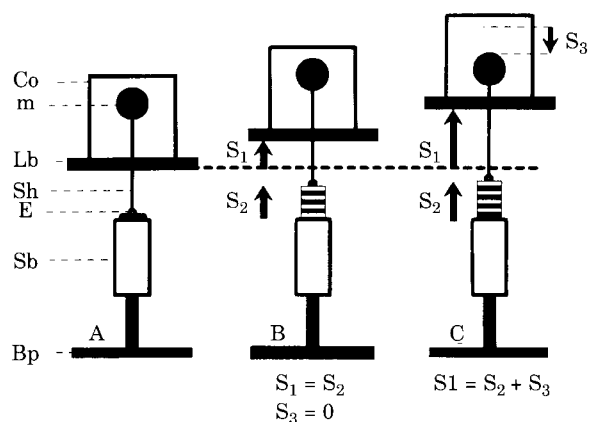

FIG. 2. The pulling experiment in principle: A, starting-position; B, movement of the lifting platform, increase of pulling force on the model corm or plant bulb; C, movement of the model against the soil resistance. Co, Container filled with sand; m, model; Lb, lifting platform; Sh, spring steel hook; E, eye for the hook; Sb, spring-balance, anchored at the base plate (Bp). S_1, lifting distance of the platform; S_2, distance of expansion of the spring-balance which is equal to the pulling force; S_3, distance of movement of the model.

relationship for channel formation, and in making estimates of the total moving work required when transporting the plant body defined distances in the soil.

METHODS

Measurement of the pulling effect

Experiment in principle (Fig. 2). The pulling work was measured using two counter movements as used for measuring the shearing strength of a soil sample (see Hartge and Horn, 1989). One of these movements was continuous, uniform and independent of the mode of action (movement of the lifting platform). The second movement (movement of the model) was caused by raising the platform.

At the beginning of the experiment the model of the plant bulb, and the container, were static (Fig. 2A). Continuous lifting of the platform (S_1) caused the spring-balance (S_2) to expand. This resulted in an increasing pulling force on the model (Fig. 2B). At this stage the distances of lifting and expansion were equal. If the pulling force became higher than the opposing soil resistance, the model was moved (S_3 in Fig. 2C). Thus, the lifting distance and spring-balance expansion were no longer equal since the latter was not reduced by the value of model movement (Fig. 2C).

Details of the apparatus. The lifting rate of the platform was 0.0106 mm s^{-1} (electric motor, Faulhuber, Aachen, Germany) and was independent of load up to 100 N over its maximum distance of 140 mm. The duration of each experiment was 220 min. Recording of the lifting movement was possible with a fibre-tip disposable pen (W. Lambrecht,

Göttingen, Germany) fixed on the platform. The spring-balance (Phywe, Göttingen, Germany) measured on a range from 0–100 N and its expansion was recorded with a fibre-tip attached to the spring-balance. The distance moved by the model (S_3, see Fig. 2C) resulted from the difference between the lifting distance (S_1) and the expansion (S_2). Checking the start of model movement was necessary because the measuring range of the spring-balance was too high to register the start of movement exactly. Therefore, a second piece of equipment was installed. A non-extensible nylon thread was attached to one end of the model. The other end of the thread was routed over a measuring scale on the outside of the container (see Froebe and Pütz, 1988; Pütz, 1992b). The movement of a point marked on the nylon thread showed exactly the start of model movement.

Overall experimental conditions. Cylindrical PVC pots (diameter 18 cm, height 20 cm) with a small hole at the centre of the base to accommodate the spring steel hook (see Fig. 2) were used as containers. A PVC globe (diameter 3 cm, smooth surface) was used as a model, with a 15 cm long hook of spring steel (non-extensible) screwed into it. For simulation of the channel effect it is necessary that firstly, the channel can be linearly compressed with little effort, and secondly, that the channel diameter remains constant during the experiment. This was achieved using specially-produced 10 cm-long tension springs (1 mm gauge silver wire), covered with transparent foil (Melita topit) so that no substratum could enter the inner channel space. In principle, any channel effect can be examined. However, we chose a 10% channel (CE = 0·1), a 40% (CE = 0·4) and a 100% channel (CE = 1·0). The selection of 0·1 and 0·4 CE appears appropriate since, as far as is known, most species have a channel effect within this range (Pütz 1992b). By adding small weights, the force necessary to compress the springs by approximately 2, 4 and 6 cm was measured. This force, determined in preliminary experiments, was subtracted from the force of the spring-balance to obtain the pulling

force actually required. The experiments took place in sand [a relatively homogenous substratum (Loam or substrata with loam usually show aggregate formation (see Scheffer and Schachtschabel, 1984, p. 127) with air cavities. It proved very difficult to obtain homogeneity and great fluctuations in measurements resulted)] from the Technische Hochschulbetriebe of the Rheinisch-Westfälisch Technische Hochschule Aachen, Germany (all particles smaller than 2 mm, see Froebe and Pütz, 1988, p 89) with a maximum water capacity of 24% (measurement to Schlichting and Blume, 1966). Our experiments were conducted with soil moisture at 40, 60 and 80% of the maximum water capacity ($\pm 5\%$ for each experiment). Soil density was obtained using thin blocks of gypsum laid on the substratum and weighted with 3 kg. In the middle of the plate was a hole equal in size to the diameter of the channel under examination. Thus, the sand around the channel could be compressed without compressing the spring. Loading commenced by putting a tension spring at the bottom of the container. One kilogramme of the substratum was added, evenly distributed and compressed as previously described for 1 min. This was repeated with another two 1 kg quantities and one 0·5 kg quantity. Thus, soil surface and spring-end were at the same level. The model was positioned by inserting the hook through the tension spring and the bottom hole, so that the globe was lying on top of the channel simulation and/or the substratum. A further 1·5 kg sand was spread over the globe and compressed. Loading the container containing no channel simulation occurred similarly, but after the fourth quantity of sand the spring steel hook of the model had to be pulled through the bottom hole using a thread.

For each channel effect (0, 0·1, 0·4) five tests were carried out for each level of soil moisture (40, 60 and 80%). However, at the various soil moisture levels the difference in movement for a given channel effect was very small, and it was thus only possible to calculate one average for each channel effect (for the total of 15 measurements). [Water added to a substratum results in a decrease of friction (Lindner and Vieweg, 1969, p 76) and to an increase in cohesion, which is important for the connection of individual grains of sand (see Scheffer and Schachtschabel, 1984, p 135). It is not possible to measure one of these forces individually (see Simmer, 1987). However, as far as we know, there is no overall factor of the ratio between friction and cohesive force. Our results show that in some cases the effect of these forces can neutralize each other.]

Measurements of the work of expansion (pushing effect)

Experiment in principle (Fig. 3). Water was pumped into a globular hollow body (balloon), positioned within the substratum, at a defined pressure increase. This pressure was a benchmark for the work required to extend the balloon in relation to soil properties and volume increase.

Experimental object: Commercial balloon catheters (Rüsch, Ch 12; Schmets, Aachen, Germany) were cut off from the balloon section. (This was necessary because expansion of the catheter-balloon was only possible in connection with material stretching, a very high pressure
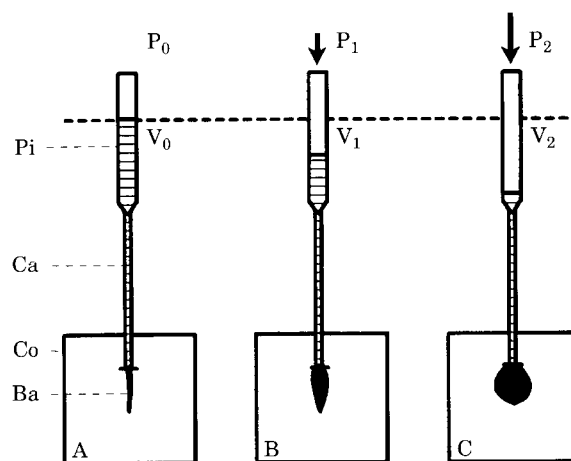

FIG. 3. The pushing experiment in principle: Pi, pipette, the hatched area shows the water level; Ca, catheter; Co, container filled with sand; Ba, balloon. Increase of pressure (P_0–P_2) leads to a water flow out of the pipette (reduction of water level V_0–V_2) into the previously compressed balloon (A), which expands against the soil resistance (B, C).

level was needed at the beginning. This would be much higher than necessary to push the soil away.) Simple globular balloons of standard form and size (Balloni, Aachen, Germany) were clamped at the location of the cut using small square PVC-blocks. The volumetric capacity of the balloons (without material stretching) was 35 ml, and at this stage the diameter was 40 mm. The experimental conditions (container, soil, moisture, density) were identical to those from the pulling measurements. During preparation of the container the balloon was inserted together with the third quantity of soil. After compacting, charging was finished as before (0·5 kg, 1·5 kg). Thus, the balloon was located in the same part of the soil in which movement of the model took place in the pulling measurements.

Experiment in detail. A pipette was filled with 40 ml water. The tip of the pipette was fixed to the catheter valve. After 30 min, the water level was measured. Next, a pressure line was fixed at the head of the pipette. This pressure line was supplied with compressed air via a precision pressure governor (Riegler, Bad Urach, Germany). The pressure was increased in 20×10^2 Pa steps (up to 1020×10^2 Pa, 1040×10^2 Pa, 1060×10^2 Pa etc.). While adjusting the pressure, the water flow was interrupted. After the next pressure level was reached, the water flow was opened and 30 min after the change in water level was measured. The experiment terminated when 40 ml water had flowed into the balloon system (35 ml into the balloon and 5 ml into the catheter system). For each soil moisture level (40, 60 and 80%) ten experiments were carried out, but no significant differences were obtained. Thus, the results of all experiments could be evaluated together and average values calculated.

RESULTS

Pulling work

The results of the pulling measurements can be seen as 'pulling curves', showing the increase in distance moved in
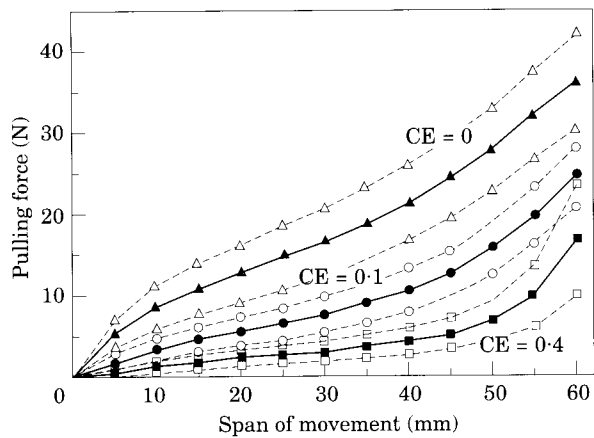
FIG. 4. Average curves for pulling movement in the model. Each average curve is drawn from 15 individual curves, standard deviation is shown by the dotted lines. CE, Channel effect.

relation to the increase of force (Fig. 4, for the various CEs). A short initial phase is followed by a continuous, linear-like rise, which eventually increases exponentially. This strong force increase occurs because, during movement, the soil beneath the model becomes compressed and soil resistance increases exponentially. This effect is intensified by the pot boundaries, as shown experimentally by Froebe and Pütz (1988).

The curves of Froebe and Pütz (1988) arise from a constant pulling force, which causes a defined movement. In contrast to this, our results show a range of movement achieved by a continuous increase in force. As a consequence, comparison of the different channel effects is only possible by calculating the work required in achieving defined ranges. Calculation is possible according to eqn (2) by the integral with limits at 0 and the distances at 20, 30, 40 or 50 mm (Riemann sum, step-function), where W is the pulling work, s the range of movement, and F the force required to achieve this range.

$$W_n = \frac{1}{2}\left[\sum_{i=1}^{n-1}(F_{i+1}-F_i)\times s_i + \sum_{i-1}^{n}(F_i-F_{i+1})\times s_i\right].$$ (2)

The results in Table 1 show that the building of a 10%

channel results in a significant decrease of pulling work. A distance of 20 mm can be achieved with a 50% smaller pulling work. This decrease is smaller the greater the distance pulled. Even so, the pulling force required to achieve 50 mm is, in the case of a 0·1 channel effect, 30% smaller than without a channel effect. A 40% channel effect leads to further reduction of the pulling force required, e.g. for a 20 mm distance about an 80% reduction occurs while for a 50 mm distance about a 59% reduction is seen. One consequence of our results is that channel formation makes soil movement easier and thus produces movement more readily. Thus, for example, pulling work equal to about 0·1 J yields a movement of 20 mm (without a channel), 30 mm (with 10% channel effect) or 40 mm (40% channel effect).

Work of expansion (pushing effect)

Measurements of volume increase depending on pressure are shown in Fig. 5A. These make it possible to obtain the pushing work as a volume integral over pressure changes (volume work). The first pressure step (in this case, up to 1020×10^2 Pa) causes a volume increase (in this case, 4·6 ml). The work W_1 required can be calculated according to eqn (3), where ΔP is the pressure difference (20×10^2 Pa) and ΔV is the volume difference.

$$W_1 = \Delta P \times \Delta V \text{ (J)}.$$ (3)

The work at the subsequent pressure steps $W_2(1040 \times 10^2$ Pa), $W_3(1060 \times 10^2$ Pa) etc., can be calculated in the same way. The work required up to a defined pressure step, or for the total pressure increase approximates to (step function) the total work at each step [eqn (4)].

$$W_{ges} = W_1 + W_2 + \dots W_n.$$ (4)

It is possible to calculate the pushing work expended before each further pressure increase step, and the dependence of volume increase of the balloon to this pushing work can be shown (Fig. 5B). After calculation of the volume of the different channels used in our pulling force experiments (length 20, 30, 40 and 50 mm; diameter 3 mm (CE = 0·1),

TABLE 1. *Pulling, pushing and moving work for different distances and different channel effects (CE), all values of work are in joules (J)*

| Work	Distance	CE = 0·0	CE = 0·1	CE = 0·4	CE = 1·0
Pulling	20 mm	0·100 ± 0·020	0·050 ± 0·020	0·020 ± 0·010	—
Pushing		- -	0·003 ± 0·001	0·024 ± 0·006	0·087 ± 0·014
Moving		**0·100**	**0·053**	**0·044**	**0·087**
Pulling	30 mm	0·190 ± 0·040	0·100 ± 0·040	0·050 ± 0·020	—
Pushing		—	0·006 ± 0·001	0·044 ± 0·009	0·134 ± 0·019
Moving		**0·190**	**0·106**	**0·094**	**0·134**
Pulling	40 mm	0·370 ± 0·060	0·210 ± 0·060	0·090 ± 0·040	—
Pushing		—	0·009 ± 0·002	0·066 ± 0·013	0·202 ± 0·024
Moving		**0·370**	**0·219**	**0·156**	**0·202**
Pulling	50 mm	0·640 ± 0·110	0·450 ± 0·080	0·200 ± 0·090	—
Pushing		-	0·012 ± 0·003	0·089 ± 0·016	0·273 ± 0·029
Moving		**0·640**	**0·462**	**0·289**	**0·273**
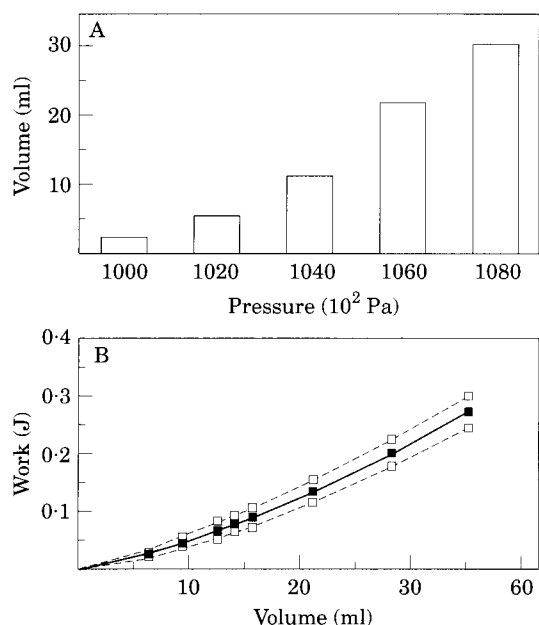
FIG. 5. A, Effect of increase of pressure on balloon volume. Average values from 30 individual curves. B, Dependence of balloon volume on work of expansion (pushing).

12 mm (CE = 0·4) and 30 mm (CE = 1·0)], the values for the work of expansion related to these channel volumes can be read in Fig. 5 B. These values are shown in Table 1. (It is possible to show the standard deviation here because the pushing work values have been determined from each of the 30 single curves and not only from the average.)

The amounts of expansion work required to form channels of equal length but of different width differ significantly from each other and show a strong increase up to 100 % channel formation. This increase is exponential. Thus, for example, forming a 30 mm long 40 % channel requires not four times, but approximately seven times as much work as a 10 % channel of the same length, whereas formation of a 30 mm long 100 % channel actually takes 22 times as much energy.

Moving work

The addition of pulling effect and work of expansion (pushing) results in a value for the total work done by contractile roots that is required for a defined movement (moving work, numbers printed bold in Table 1). In every case this total work decreases if a channel is involved in the moving process. In some cases a very small amount of pushing energy is enough to allow a considerable reduction of the pulling required. Thus, for example, 0·003 J required to form a 20 mm long 10 % channel compensates for about 0·05 J of pulling (more than tenfold). This ratio of economization can even be found at a distance of 50 mm, where the energy required to form the 10 % channel (0·012 J) conserves 0·19 J. Forming a 40 % channel also leads to a reduction in the value of pulling force required. Thus, a pushing force of 0·066 J at a 40 mm distance is less than one-

quarter compared with the pulling energy that is saved (0·28 J).

The energy required to form a 20 mm-long 100 % channel is not much lower than the pulling force which would be required to achieve this distance without a channel. However, increasing the distance moved results in a saving of energy. For example, formation of a 50 mm long 100 % channel requires only about 43 % of the required pulling force.

Energetic comparison of the moving work required makes two things clear: (*a*) for smaller movements (20–30 mm), formation of a 10 or 40 % channel is, energetically, particularly favourable; (*b*) for longer movements (50 mm and more) formation of a 100 % channel is, energetically, the most advantageous.

DISCUSSION

Froebe and Pütz (1988) have shown experimentally the importance of various parameters in underground movement. In general, they found that different soil types as well as specific soil conditions (moisture and density) influence the extent of underground movement. Thus, for instance, model movement in a hard, strong compressed soil becomes very small. On the other hand they have shown the importance of plant parameters (size, form and surface of the model) for the success of underground movement. They have introduced the channel effect and discussed its role in the efficiency of pulling movements, but did no experiments on this theme. Our present results shown here are able to confirm the importance of a channel effect from a biological standpoint. Our experiments have been designed to help understand the role of a channel effect in general. However, it should be mentioned that further experiments still have to be carried out, so that particular questions could be answered, concerning more realistic soils which contain silt and clay, which are compressed to different extents. It would also be instructive to use a natural bulb (see Pütz, 1992*b*). Further experiments may usefully include methods and approaches adopted by soil physicists when studying forces that displace soil during root growth (e.g. Bengough and Mullins, 1990) and to apply appropriate theories of soil mechanics (e.g. Dexter, 1987).

All this makes clear that the absolute order of magnitude of our findings greatly depend on our standard parameters. Thus, the pulling work values directly measured for several species show relatively large differences (according to the species 0·1–1·6 J, Pütz, 1992*b*), depending on various soil factors and the size and form of the plant body. Our present results are thus of greater significance with respect to the relative values obtained than in the absolute values. In principle, three interesting facts are shown concerning the biological importance of a channel effect: (1) in general, formation of a channel results in a movement requiring less work. This obvious statement becomes more significant when it is recognized that a very small amount of energy used in pushing is able to compensate for a relatively high pulling force. It thus becomes clear that species with contractile roots also normally show a channel effect. Up to

now the only known exceptions are a few species within the Aroideae, e.g. *Amorphophallus bulbifer*, *Sauromatum guttatum* (Pütz, 1992) and *Zantedeschia alba-maculata*. (2) Our results show great differences in value between pulling and pushing forces. Thus, for example, the total energy for movement with a 50 mm long 100% channel is reduced by more than half when compared with a 50 mm movement without a channel. The reason for these differences is the direction of soil compression. Lateral soil compression in general is less than vertical soil compression (factor: 0·2–0·7, Scheffer and Schachtschabel, 1984, p 137). More important is the exponential increase of soil density beneath the plant body for continuously increasing moving distance, so that vertical pulling work also increases exponentially. However, soil density during pushing is constant for each root sector, so that the increase in pushing work for longer channels is linear. It should be mentioned that the difference between pulling and pushing in the case of 40 or 50 mm long channels might be even higher, because our calculation does not take account of the specific channel form. (Pushing work was measured in our experiments by the expansion of a globular body with a diameter of 40 cm. The channel volumes were calculated as cylindrical bodies with a defined maximum lateral extension. A calculated correction based on the pushing work estimated as necessary for the defined maximum lateral extension and linear interpolation would lead to even smaller values of the pushing force.) (3) Finding the total amount of moving work in relation to channel width and moving distance makes it possible to characterize, from an energetic point of view, the optimum moving systems: at short distances (up to 30 mm) small channels (0·1 and 0·4 CE) seem to be efficient, whereas at longer distances (> 50 mm) the 100% channel is superior. It appears significant that these moving systems commonly appear in nature: (*a*) many monocotyledonous species have contractile roots with a small channel effect of approx. 10–40%, and these species show only small amounts of underground movement (10–25 mm, Pütz, 1992*b*). Such movements are important for depth regulation, for example, to compensate for growth. There are some indications that individuals located near the soil surface increase their channel effect, partly by increasing root diameter (*Phaedranassa chloracea*, Rimbach, 1938) and partly by reducing the diameter of the plant body (*Crocus sativus*, Negbi *et al.*, 1989). (*b*) 100% channels are comparatively rare. Turnips of the Apiaceae, which seem to be contractile (Berkemeyer, 1928) and have a diameter of 30 mm and more, can be interpreted in this way. However, detailed examinations of the Apiaceae and other dicotyledonous families are still lacking. Up to now, the 100% channel appears to apply to only a handful of species (*Brodiaea capitata*, Rimbach, 1902; *Triteleia hyacinthina*, Smith, 1930; Pütz, 1992*a*; *Oxalis pes-caprae*, Galil, 1968; Pütz, 1994; *Muscari parviflorum*, Galil, 1983). In all these cases the function of the movement is the vegetative spreading of lateral buds. These movements are 5 cm and more. In the case of *Oxalis pes-caprae*, Galil (1968) reported a maximum movement of 47 cm. Finally, it must be supposed that seedlings, especially from geophytes, often have a 100% channel. This seems necessary to reach greater depth during

penetration, where the seedlings can survive their first unfavourable season in safety. A few measurements show movements of 60–100 mm and a high channel effect (*Chlorogalum pomeridianum*, Jernstedt, 1984; *Nothoscordum inodourm*, Pütz, 1993), but intensive studies still have to be carried out.

In this paper the natural conditions of the soil have not been considered. However, underground movement can be strongly hindered, e.g. by the natural soil structure. Thus, Rimbach (1896) describes individuals which do not reach their optimum depth because of hindrance, e.g. by stones situated beneath them. A counter-effect is produced by cavities in the soil, making movement easier. Cavities and soil loosening occur naturally, e.g. by decomposition of dead roots or the activity of worms. With respect to natural conditions it is clear that efficiency of channel formation must be considered not only from an energetic, but also a functional point of view. For instance, in stony soils 100% channel formation may be the only possibility for plants to make any movement or to overcome hindrances. Ecologically-oriented investigations taking account of the survival of plants with the help of contractile roots seem necessary. However, experimental simulation may also be important if it proves possible, in the future, to prepare standardized heterogenous soils and apply the results obtained to natural conditions.

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