Measurement of the pulling force of a single contractile root

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A technique is described that can be used for direct measurement of the force of a single contractile root. This lifting technique has been tested on five species. It is shown that the results from direct measurement are in general agreement with those obtained with an indirect measurement. This new technique makes it possible to measure the pulling force of plants with specialized movements. e.g., *Triteleia hyacinthina*, in which contractile roots produce a channel for the movement of the offset. Although *Triteleia* contractile roots have what has been described as a 100% channel effect, measurements with the lifting technique show that a pulling force can, indeed, be measured.

Key words: contractile root(s), monocotyledons, root contraction, plant movement, *Triteleia hyacinthina*, *Sauromatum guttatum*.

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L'auteur décrit une technique qui peut être utilisé pour la mesure directe de la force d'une seule racine contractile. Il a essayer cette technique sur cinq espèces de plante. Les résultats obtenus concordant généralement avec ceux obtenus avec une méthode indirecte. Cette nouvelle technique permet de mesurer la force de tension des plantes possédant des mouvements spéciaux, e.g., *Triteleia hyacinthina*, chez qui les racines contractiles produisent un canal pour le mouvement des ramifications. Bien que les racines contractiles du *Triteleia* possèdent ce qui a été décrit comme un effet de canal à 100%, les mesures effectuées par soulèvement montrent qu'on peut effectivement mesurer une force de tension.

Mots clés : racines contractiles, monocotylédones, contraction racinaire, mouvement végétal, *Triteleia hyacinthina*, *Sauromatum guttatum*.

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Introduction

Bulbous and cormous plants (geophytes) are adapted to survive unfavourable seasons such as cold winters or dry and hot summers below the soil surface. Their geophilous organs, with renewal buds, can be found at specific depths ("physiological depth," Galil 1958). Physiological depth is reached actively in different ways. It may be simply by growth or, less simply, with the help of specialized "remoters" (Galil 1980). Another possibility for movement is by contractile roots. In the latter case, movement of underground organs will occur if soil resistance is overcome. This can be accomplished by building up a sufficient pulling force (Rimbach 1898; Arber 1925) or by formation of soil channels, produced by thickening of contractile roots, through which underground organs are transported ("pioneer roots," Galil 1980; "channel effect," Froebe and Pütz 1988).

Sauromatum guttatum produces contractile roots at the top of the corm (Scott 1908). These contractile roots grow downward around the corm. Figure 1 shows the cryptocorm of *Sauromatum guttatum* at the beginning of pulling activity (Fig. 1A) and the same individual 17 weeks later (Fig. 1B). Comparison of the distance between the top of the corm and the soil surface in Figs. 1A and 1B shows that downward movement of the corm has occurred. In this species there is no channel effect; the corm must be moved down against the full soil resistance by the pulling activity of contractile roots (Fig. 1C).

The opposite extreme is seen in *Triteleia hyacinthina* (Lindl.) Greene (= *Brodiaea lactea* (Lindl.) Wats.) where contractile roots are produced only on offsets and never on parent corms (Smith 1930). The movement of these offsets is horizontal, along the direction of the contractile root (Figs. 2A and 2B; see also Pütz 1991). Since the diameter of the offset does not exceed that of the contractile root, movement occurs within the tube or channel formed by soil displacement during contractile root growth (Fig. 2C). There is no soil resistance to movement, which has led to the designation "100% channel effect" of contractile roots for this type of movement (Froebe and Pütz 1988).

Galil (1980) suggests that the most common function of contractile roots is to create a channel through which the remoter advances. He hypothesizes that the pulling effect of the root is secondary to the pushing force of the remoter. According to this hypothesis, the pulling force of contractile roots with a 100% channel effect should approach zero. Offset movement in *Triteleia hyacinthina* appears to fit the Galil model, with the pulling force of *Triteleia* contractile roots predicted to be near zero. At the very least, the force of *Triteleia* contractile roots would be expected to differ markedly from contractile roots of *Sauromatum*, which must exert sufficient force to overcome soil resistance.

Until recently, the only method to measure the pulling force of roots was an indirect approach (Froebe and Pütz 1988). This procedure is dependent on bulb and root growth under near-natural conditions. First the natural extent of bulb or corm movement into the ground by contractile roots is measured. This movement is then simulated, using standard weights, hung at the corm, to effect comparable displacement. If soil conditions are similar, comparison of simulated and natural movement is possible. To reach a specific depth, a specific pulling force will be necessary, created either by contractile roots or by standard weights. This indirect method results in specific data on the total pulling force that must have been exerted by all roots to move the corm or bulb to a particular position in the soil (Pütz 1989). It is not possible using this method to measure the pulling effect of a single contractile root, although a per root value can be calculated. Moreover, it is impossible to measure the pulling force of contractile roots for plants that have certain types of specialized movement, such as the lateral movement of *Triteleia* (Pütz 1991).

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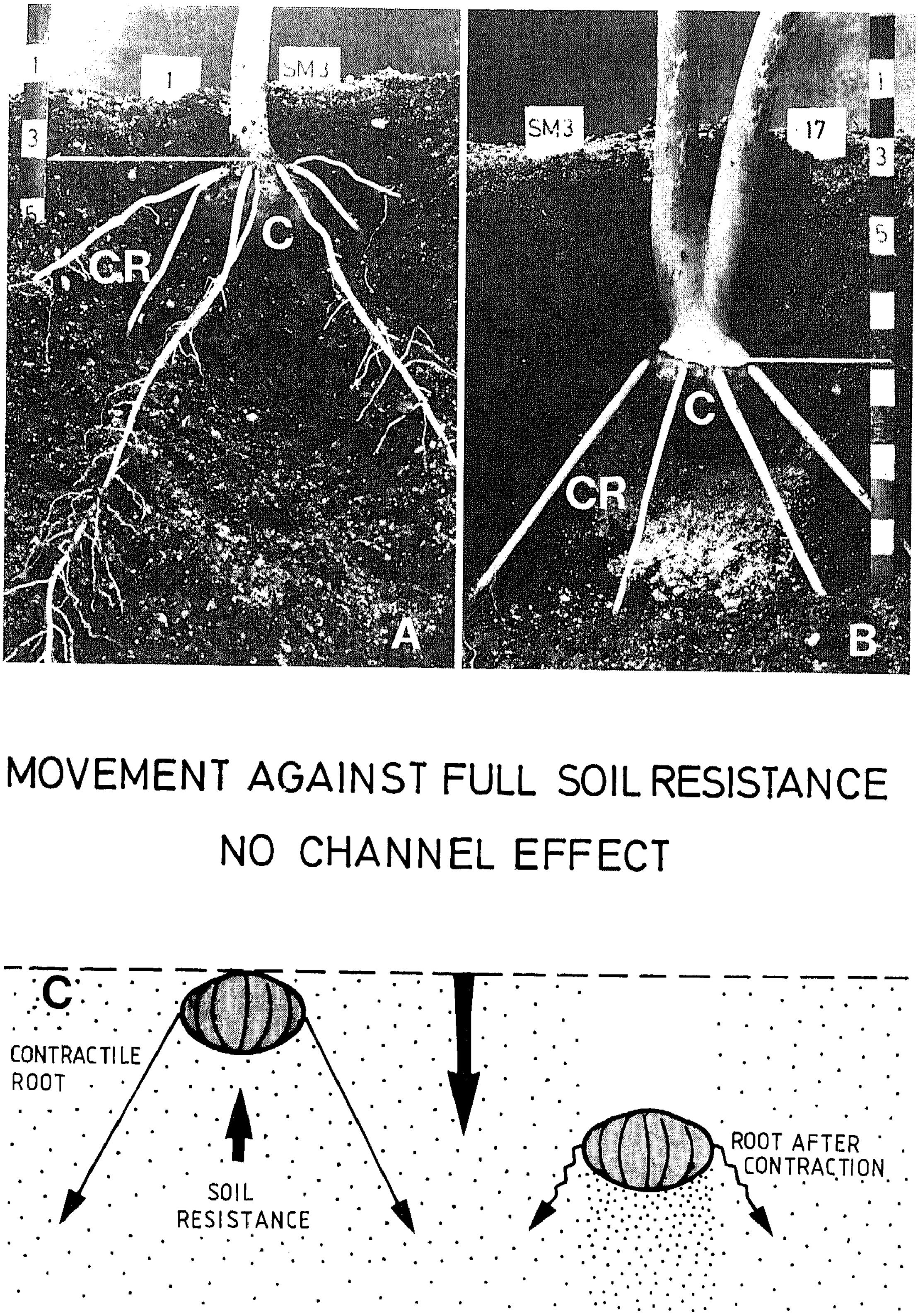

FIG. 1. Movement of *Sauromatum guttatum*. (A) Side view of the cryptocorm at the beginning of pulling activity. (B) Same corm, 17 weeks later. The white lines show position of the top of the corm to soil surface (scale graduation in centimetres). (C) Schematic explanation for movement against full soil resistance. Contractile roots produce no channel effect. CR, contractile root; C, corm.

This paper introduces a new technique for direct measurement of the pulling force of a single contractile root. Comparison with the results of the indirect method is made. Results are also reported for application of the indirect method to the 100% channel species, *Triteleia hyacinthina*, and discussed in terms of Galil's (1980) hypothesis.

Materials and methods

Plant material

Plant material was chosen with regard to the extent of the estimated channel effect: *Triteleia hyacinthina* (Lindl.) Greene (Alliaceae), Botan. Garten Wuppertal (channel effect: 100%); *Asphodelus aestivus* Brot. (Asphodelaceae), Cinque terre, Italy (channel effect: 60%);

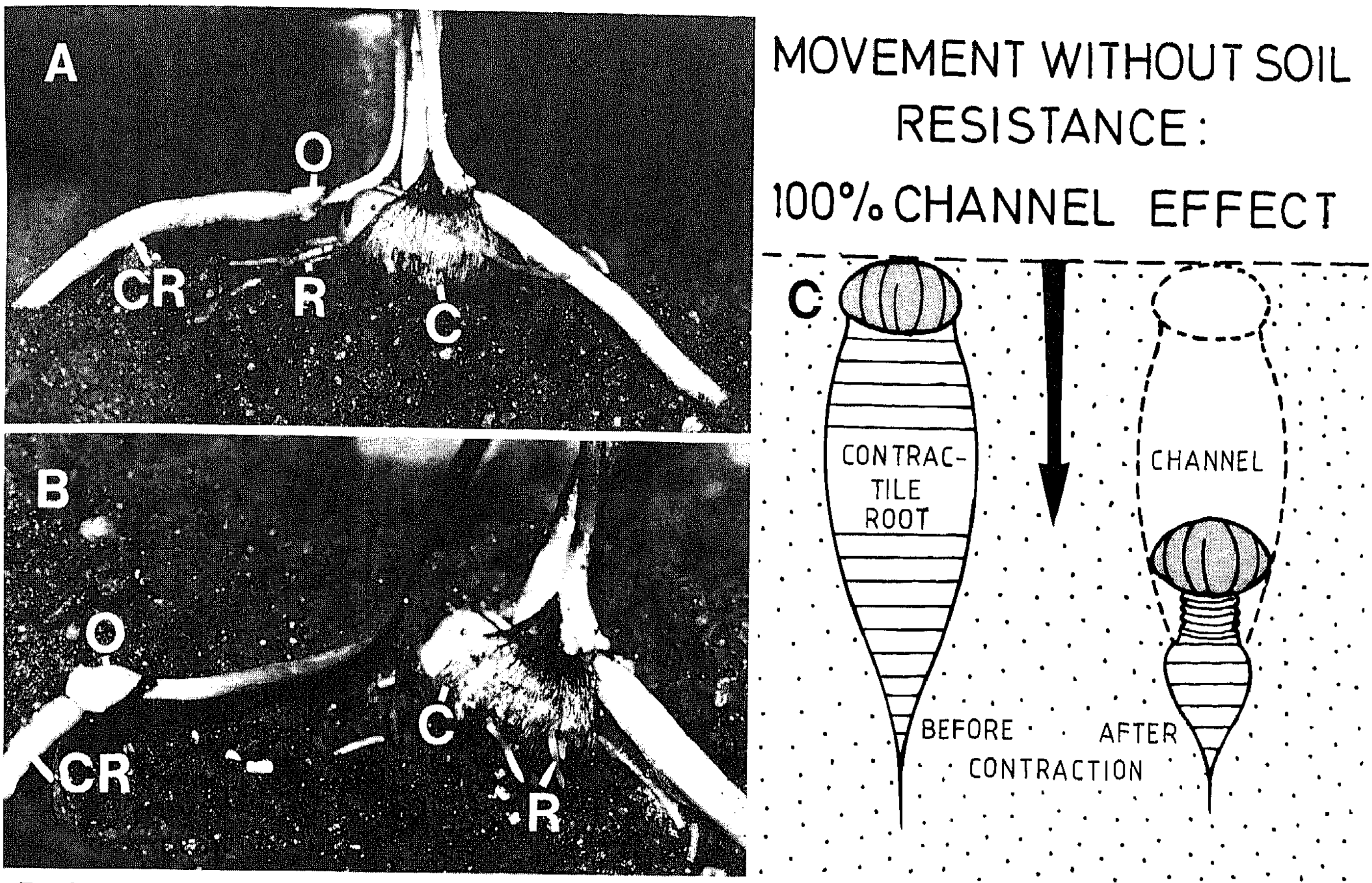

FIG. 2. Movement of *Triteleia hyacinthina*. (A) Side view. (B) Side view (2 weeks later than A). (C) Schematic explanation for movement without soil resistance. While shortening, the contractile root produces a soil channel for the movement of the corm. CR, contractile root; C, corm; O, offset; R, "normal" root (not contractile).

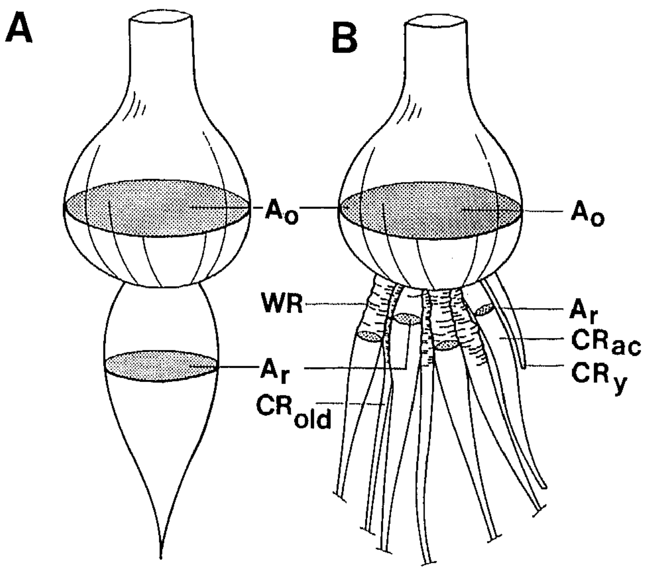

FIG. 3. Schematic explanation for the calculation of the channel effect. The stippled surfaces are the ones used for calculation (see text). (A) Species with only one contractile root. (B) Species with several contractile roots. A_0, cross-sectional area of the geophilous organ; A_r, cross-sectional area of the root; CR, contractile root (*ac*, active; *y*, young, before contraction; old, after contraction); WR, wrinkled surface as a characteristic feature for root contraction.

Acidanthera bicolor Hochst. (Iridaceae), Bot. Gart. R.W.T.H. Aachen (channel effect: 30%); *Arum italicum* Mill. (Araceae), Cinque terre, Italy (channel effect: 20%); *Sauromatum guttatum* (Wall.) Schott (Araceae), Bot. Gart. R.W.T.H. Aachen (channel effect: 0%).

Procedure for calculation of the channel effect

In most cases geophilous organs are transported along the direction of contractile root growth and a channel effect exists. This channel effect (CE) is related to the maximum cross-sectional area (A_0) of the geophilous organ (bulb or corm), the cross-sectional area of the pulling roots (A_r), and the number of pulling roots (N_r). It can be calculated by the following formula for bulbs or corms with a single contractile root (see Fig. 3A)

$$[1] \quad CE = \frac{A_r}{A_0}$$

The cross-sectional areas (A_r and A_0) were calculated according to the formula

$$[2] \quad A = \pi\,(d/2)^2$$

where d is the diameter of the root or corm that was determined by direct measurement. When the diameter of the root exceeds that of the organ, the channel effect is defined as 100% (e.g., *Triteleia hyacinthina*).

In many species several contractile roots develop successively during the period of vegetation growth (Pütz 1991). Therefore, one can find old, fully contracted roots; active, contractile roots; and young, not yet contractile roots at the corm or bulb (see Fig. 3B). In these cases it is a useful approach to estimate that at a given time during the pulling period about half of all contractile roots ($N_r/2$) are participating in forming a channel.

$$[3] \quad CE = \frac{A_r \cdot N_r}{A_0 \cdot 2}$$

Equation 3 results in the CE for species here with several contractile roots (*Arum*, *Asphodelus*, *Acidanthera*). For convenience, the channel effect is rounded to the nearest 10%.

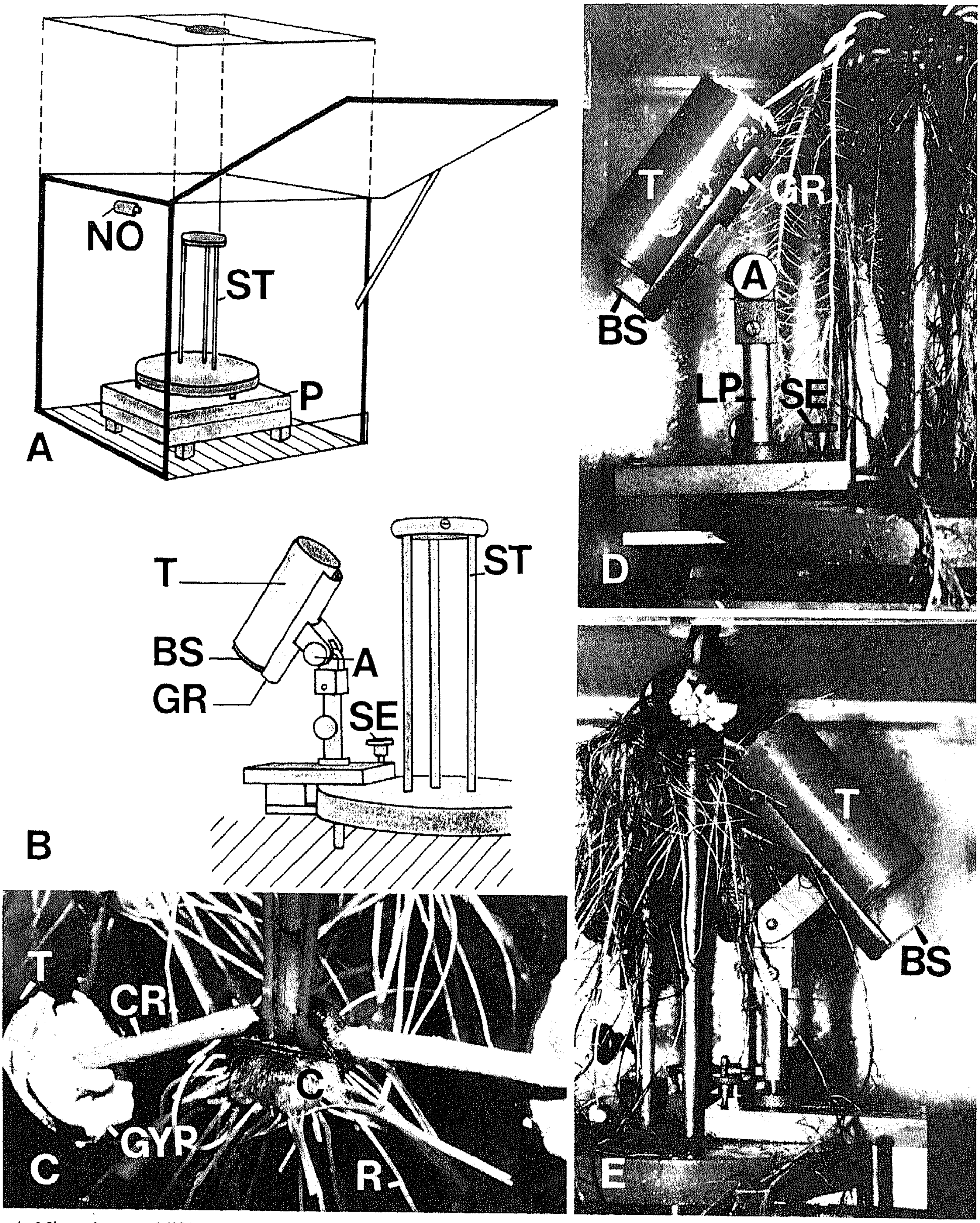

FIG. 4. Mist culture and lifting technique. (A) Culture chamber. (B) "Tube-lifting" equipment at the beginning of an experiment; tube is resting at the bearing surface. (C) View inside the culture chamber of *Triteleia*. (D) View of the culture chamber of *Sauromatum* 40 days after beginning of the tube-lifting experiment: distance between bottom of the tube and bearing surface shows pulling activity of contractile root. (E) View of the culture chamber of *Acidanthera* 30 days after beginning of the tube-lifting experiment. A, articulation; BS, bearing surface; C, corm; CR, contractile root; GR, guide rail; GYP, "packing ring" of plaster of paris; LP, lifting post; NO, nozzle for mist spray; P, pedestal; R, "normal" root (not contractile); SE, setscrew; ST, stand; T, tube.

Growth conditions

The basic requirement is to cultivate plants without soil. For this purpose the apparatus of Areichovsky (see Grafe 1924) has been automated and converted to a mist culture system (see, e.g., Clayton and Lamberton 1964).

The plant is placed on a stand (ST in Fig. 4A) and fixed in place with coated wire. The stand is put on a pedestal (*P*) in the culture chamber (Fig. 4A). This pedestal is composed of several plates and is, therefore, adjustable in height. The dimensions of the culture chamber are 300 × 300 × 300 mm. It is made of Perspex with one hinged side. There is an inlet for a mist spray nozzle (NO, Fig. 4A) and an outlet for the nutrient solution collected at the bottom of the chamber. A removable two-piece top allows access from above during plant growth; the top of the chamber contains an opening through which upper plant parts emerge from the chamber. To darken the roots, the chamber is placed in a wooden frame. Plants are sprayed with Knop's nutrient solution (Mohr and Schopfer 1979, p. 244) for 15 s at hourly intervals. Three of these chambers have been manufactured and were placed in the laboratory near the windows. Temperatures were ca. 18°C at night and 23–35°C during the day. Plants grew best from April to September and measurements were made during this time span in the years 1985–1989.

The lifting technique[1]

Suitable roots[2] were introduced into small plastic tubes (100 mm length × 20–40 mm diameter, with bottom, see Fig. 4B) filled with substratum (a mixture of sand and loam). Masses from 50 to 200 g were obtained by using tubes of a different diameter. To prevent roots from pulling themselves out of the tubes when contracting, they were fixed to the tubes using a "packing ring" of plaster of paris (Fig. 4C). Roots were placed at least 20 mm into the substratum and apical growth of the root within the tube was still possible (apical growth of the root within the tube does not affect the lifting movement subsequently measured). Roots were also marked with ink to detect any movement relative to the packing ring.

Correct orientation of the tube relative to the root axis was made possible by a specially constructed support in which tube height and angle could be adjusted (LP, Fig. 4B). The tube rested against a guide rail (GR) and could thus be displaced along the GR by root contraction. To minimize frictional resistance the surface of the GR is more concave than the roundness of the tube. The occurrence and extent of contraction were determined by measuring the change in distance (mm) between the bottom of the tube and the bearing surface (BS) over the course of an experiment. Measurement of the force of a single contractile root took about 40 days. There was no visible degeneration of the root owing to the packing ring or culture conditions for at least 8 weeks.

Calculation of pulling force

[4] force or weight (N) = mass (kg) × acceleration (= 9.81 m/s^2)

Using [4] the pulling force of the root resulting in tube movement can be calculated. The lifting force should be calculated as the force of gravity on the tube mass, multiplied by the cosine of the lifting angle. For example, if the lifting angle is 45°, then the lifting force owing to gravity is 0.707 of the weight of the tube because the guide rail is carrying the remaining 0.293 of the weight. However, control experiments[3] with a spring balance showed a sliding force that was very similar to the weight of the tube (calculated by eq. 4):

tube mass (g)	80	100	120
sliding force (J)	0.8	1.0	1.2
tube weight (N) (by eq. 4)	0.785	0.981	1.177

This implies that there is a frictional resistance of the apparatus of about 30% of the tube's weight.

[1]Inspiration for this lifting technique was a photograph in Zimmermann et al. (1968, p. 102, Fig. 4). The legend to this figure states: "A free-hanging aerial root, planted in a pot with soil, contracted sufficiently to lift the pot off the ground."

[2]Suitable root means a root just before contracting (criterion: expansion of the proximal root zone; see Pütz et al. 1990, p. 150).

[3]Support angles used in control experiments were similar to the angles used in the lifting experiments: 40°–60°.

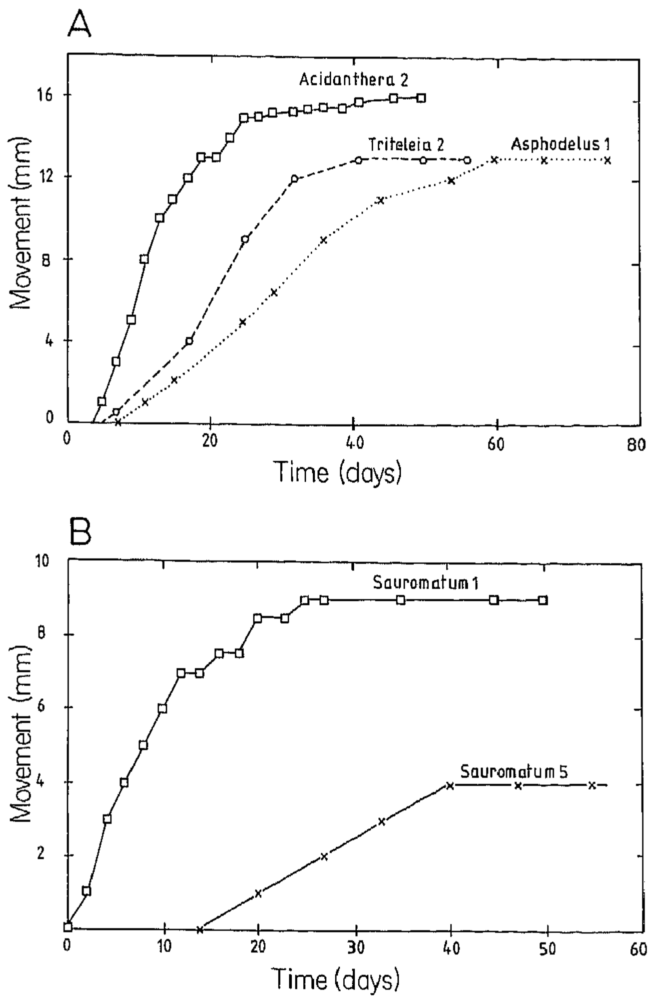

FIG. 5. Lifting movement (displacement) of tubes owing to the pulling activity of a contractile root. (A) Lifting masses are 82 g for *Asphodelus* 1 and *Triteleia* 2 and 93 g for *Acidanthera* 2 (see Table 1). (B) Tube mass of *Sauromatum* 1 is 92 g and tube mass of *Sauromatum* 5 is 160 g.

To determine the work (J) of a pulling root, the distance of movement (m) is multiplied by the calculated force (N). Work divided by pulling time (s) yields the power (W) of a single root. Initial measurements were based on applied mass (tubes) of about 90 g. For *Sauromatum guttatum*, weights were gradually increased to determine the maximum pulling force of a contractile root.

Results

Examples of end points of tube-lifting experiments are shown for *Sauromatum guttatum* (Fig. 4D) and *Acidanthera bicolor* (Fig. 4E). The extent of movement is measured as the distance from the bottom of the tube to the bearing surface (BS). Since the starting point was the tube resting on the BS, this span clearly demonstrates the pulling force of a contractile root. Moreover, continuous observation allows one to follow the kinetics of lifting movement in time. As seen in Fig. 5A, *Acidanthera bicolor* 2, *Asphodelus aestivus* 1, and *Triteleia hyacinthina* 2 show a comparatively powerful beginning of root contraction, which eventually reaches a plateau. The lifting mass of these examples is 82 g for *Asphodelus* 1 and *Triteleia* 2 and 93 g for *Acidanthera* 2. Individual values of the measured roots of all plants are given in Table 1, where the time span of movement is the time in days from the first lifting movement to the attainment of the plateau.

Measurements from increasing tube mass allow calculation

TABLE 1. Results of measurements of contractile root activity using the lifting technique

	Sample No.	Tube mass (g)	Span of movement (mm)	Time span of movement (days)	Pulling force (N)	Work (J)	Power (10^{-8} W)
Acidanthera bicolor	1	92	8	30	0.90	0.007	0.27
	2	93	16	40	0.91	0.015	0.40
	3	97	8	37	0.95	0.008	0.25
Asphodelus aestivus	1	82	13	51	0.81	0.011	0.25
	2	92	9	39	0.90	0.008	0.24
	3	93	8	47	0.91	0.007	0.17
Arum italicum	1	88	6	35	0.86	0.005	0.17
	2	97	3	32	0.95	0.003	0.11
	3	102	3	30	1.00	0.003	0.12
	4	140	—	—	1.37	—	—
Sauromatum guttatum	1	92	9	25	0.90	0.008	0.37
	2	99	8.5	30	0.97	0.008	0.31
	3	116	9	26	1.14	0.010	0.45
	4	148	5	25	1.45	0.007	0.32
	5	160	4	22	1.57	0.006	0.32
	6/7	178	—	—	—	—	—
	8/9	182	—	—	—	—	—
Triteleia hyacinthina	1	32	15	30	0.31	0.005	0.19
	2	82	13	35	0.80	0.010	0.33
	3	133	10	28	1.30	0.013	0.54

NOTE: Each value is based on the measurement of a single contractile root (see Materials and methods section for calculations of work and power).

TABLE 2. Comparison of the results of work of a single contractile root determined by the indirect apparatus and the lifting technique

	Indirect	Lifting
Acidanthera bicolor	0.017	0.007
	0.014	0.015
	0.028	0.008
Average	0.020±0.006	0.010±0.004
Ratio	1:0.5	
Asphodelus aestivus	0.014	0.011
	0.019	0.008
	0.011	0.007
	0.012	
	0.017	
	0.025	
Average	0.016±0.005	0.009±0.002
Ratio	1:0.56	
Arum italicum	0.012	0.005
	0.006	0.003
	0.008	0.003
Average	0.009±0.003	0.004±0.001
Ratio	1:0.44	
Sauromatum guttatum	0.026	0.008
	0.031	0.008
	0.007	0.010
	0.010	0.007
	0.016	0.006
Average	0.018±0.009	0.008±0.001
Ratio	1:0.44	
Overall average	0.016±0.007	0.008±0.003
Ratio	1:0.5	

of the maximum force a contractile root can exert. In Fig. 5B, *Sauromatum* 1, with a tube mass of 92 g, corresponds to the roots shown in Fig. 5A. The second curve in Fig. 5B (*Sauromatum* 5) shows the lifting movement of a heavier tube (160 g). The shape of the curve is basically similar but the slope is less and the plateau is reached at a lesser distance. There was no lifting when the tube mass was heavier than 160 g (measurement of roots 6–9, see Table 1). The data of *Sauromatum* in Table 1 show that an increase in tube mass leads to a decrease of the lifting movement. It is interesting to note that although the forces rise continuously (see Table 1, *Sauromatum*), the magnitude of variation for the values of work is small.

Discussion

It is now possible to obtain physical data on contractile roots in two different ways. With the indirect apparatus (Froebe and Pütz 1988), downward movement of a plant into the ground can be measured. Cumulative physical data of all contractile roots of a single plant are obtained by this indirect means. Data for single roots can be determined by calculation only (Pütz 1989). With the direct method, the lifting technique described here, forces and movement resulting from activity of a single contractile root are measured. Moreover, the lifting technique is suitable for characterizing the pulling force of species that show specialized movement, e.g., *Triteleia hyacinthina* (Smith 1930; Pütz 1991).

Nonetheless, it can be argued that the lifting technique is very artificial, using as it does mist culture without soil and measuring upward movement. It is clear that results obtained by the lifting technique must be corroborated by comparison with a more natural situation. To be valid, the lifting technique

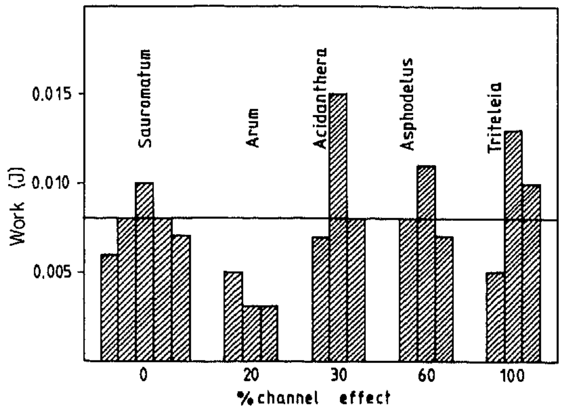

FIG. 6. Work of a single contractile root relative to the channel effect. Each bar represents the measurement of a single root. The line at 0.08 J represents the average of all measurements.

should provide results that are comparable with other methods for a single species and for relative comparisons between species. Species of *Acidanthera*, *Asphodelus*, *Arum*, and *Sauromatum* have been tested by both methods (Pütz 1989), and it is possible to compare results for work[4] performed by a single contractile root of these species. Comparisons are shown in Table 2.

A comparison of the average value of all measurements shows that the indirect method consistently produces the higher value (ratio of indirect to lifting 1 to 0.5). However, standard deviations show that this difference is not significant. Nonetheless, this difference may be due to the standardization of the indirect method and the calculation necessary in the indirect method to obtain results for single contractile roots. On the other hand, the lifting technique (direct method) is very artificial, possibly the frictional force of the guide rail is larger in the very slow pulling process of root contraction. This effect, which is not considered in [4], may increase lifting force. So it is not clear which average value is more realistic. Both methods characterize the quantity of work of a contractile root to be in the same order of magnitude. Moreover, the ratio of results from the two methods for each species is quite similar. Nevertheless, these ratios are based on only three to six measurements, so definitive conclusions cannot be drawn. Since all species show a ratio of about 1:0.5, it can be assumed that no single species suffers disproportionately by growth in mist culture, and measurements of the physical data may be quite realistic.

Finally, it is reasonable to compare physical measurement results taking into account the channel effect discussed above. Figure 6 shows that there is no relationship between the work of a single contractile root and the extent of the channel effect. It is not yet possible to analyze maximum root forces relative to the channel effect, since maximal root forces have only been determined for *Sauromatum*. However, even for *Triteleia*, with a 100% channel effect, pulling force can be measured. This force is generally similar in magnitude to the forces measured for the other species (Table 1). So, it can be stated that contractile roots that form channels are not incapable of exerting a distinct pulling force. Contrary to Galil's hypothesis (1980), such channel-forming roots exert forces of comparable magnitude with nonchannel formers. The pulling effect thus seems to be quite important even for plants that show a 100% channel effect.

[4]Work is taken for comparison because the results of *Sauromatum* (Table 1) show that the values of work are rather constant even when pulling force increases continuously.

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