Underground Plant Movement

I. The Bulb of *Nothoscordum inodorum* (Alliaceae)

N. Pütz
Botanisches Institut, Abteilung Morphologie, Technische Hochschule Aachen, FRG

Received: February 18, 1993; Accepted: April 6, 1993

Abstract

A special preparation method makes it possible to observe the underground bulb movement of *Nothoscordum*. This movement is effected by contractile roots. Straight ahead movement, which seems to be typical for many bulbous plants, is only exceptionally seen in *Nothoscordum*. Bulb movement in *Nothoscordum* occurs by tilting and twisting, effected by the pulling force of contractile roots on one side of the bulb. Also, vegetative dispersal of lateral bulbs (daughter bulbs) caused by the pulling force of contractile roots can be documented. Finally, starting from the seedling, the overall bulb movement can be demonstrated, showing how the plant penetrates the substratum thus reaching the optimum depth.

Key words

Contractile root, root contraction, plant movement, *Nothoscordum*, Monocotyledons.

Introduction

Contractile roots develop a pulling force (Rimbach, 1898; Pütz, 1992). This force has an effect upon the underground plant body (e.g. bulb, corm etc). Under certain conditions (e.g. low soil resistance, see Froebe and Pütz, 1988) underground movement of the storage organ occurs. The functions of this plant-movement are (1) depth regulation of the storage organ for surviving unfavourable seasons like cold winters or dry summers (de Vries, 1880; Rimbach, 1898, 1902), (2) vegetative dispersal of lateral buds (daughter bulbs etc, Rimbach, 1902; Smith, 1930; Galil, 1965, 1985) and (3) downward movement of the seedling (Rimbach, 1898a; Jernstedt, 1984).

Direct observation of underground movement has not been successful up to now, only the position of the storage organ in the soil has been demonstrated (e.g. Rimbach, 1898; Arber, 1925; Troll, 1937–43) or, at best, a schematic reconstruction of movements has been given (Pütz, 1991). A precise functional analysis is only possible if the process of movement can be observed directly in the soil.

Contractile roots of bulbous plants have been investigated from different perspectives (e.g. *Cooperia* by Church, 1919; *Hyacinthus* by Wilson and Honey, 1966; *Narcissus* by Chen, 1969; *Eucomis* by Reynecke and van der Schijff, 1974; *Allium* by Deloire, 1980). However, the result of contractile root activity – plant movement – has not been taken into account. Using a special preparation technique, movement of a bulb in the soil can be described and analysed. So, in this paper the functional aspect of the contractile root becomes the main point of interest.

Material and Methods

For this examination bulbs of the Mexican *Nothoscordum inodorum* (Ait.) Nichols [Botanical Garden R.W.T.H. Aachen] were used.

15 planting pots (Fa. Richard Sankey & Son, LTD. Nottingham, England, Vol. 10 l) were used. A large aperture was cut out at the side. During cultivation this aperture was covered by a longitudinally-halved pot (Figs. **1A, B**). These test containers were filled with riddled sand/loam mixture (see Froebe and Pütz, 1988). In each container one bulb was planted approx. 10 mm under the soil surface. Plants were cultivated in a greenhouse for one year. Minimum temperature varied from 14 °C at night to 20 °C during the day (on hot summer days maximum temperature were measured up to approx. 35 °C, even in the shade). The plants were illuminated for 12 h daily with plant lamps (Osram, power star HQI-T 400 W/DH) to supplement daylight. During examination the longitudinally-halved pot of the test container was removed (Fig. **1B**) from the aperture. The substratum was removed (using a thin wooden stick and a brush) to expose the bulb and proximal root parts (Fig. **1C**), but without removing the soil supporting the plant. Bulb and root parts were cleaned with a small jet of water (Primo disposable Syringes 20 ml and disposable needle 0.4 × 21 mm, hospital supplies). Beside the plant a scale was carefully inserted measuring depth. In Figs. **3 A–C** it can be seen that the insertion depth of the scale varied relative to the white control line. This was necessary to take account of any possible hindrance in the soil. If the scale was inserted too strongly against any hindrance, soil sliding or root damage might have occurred, therefore, this was left off. When planting the bulb, a strip of aluminium (10 mm wide, 5 mm high, 30 mm long) was located a few cm from the bulb for use as a control mark (C in Fig. **1D**). Any

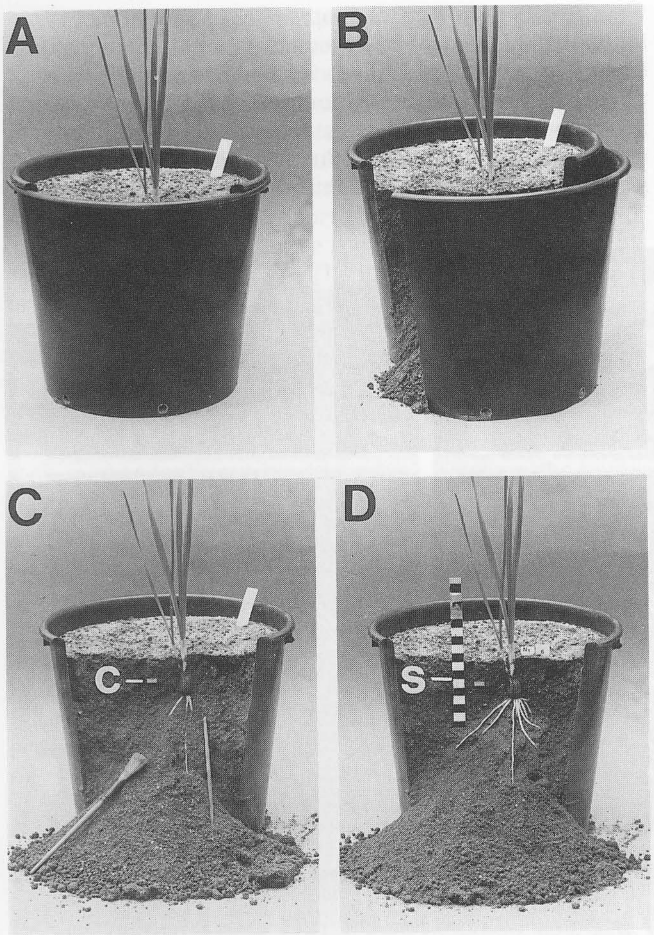

Fig. 1 The preparation method for analysing the underground movement of cryptocorms. The test container has a large aperture, which is covered during cultivation by a longitudinally-halved pot (**A, B**). Every 1–3 weeks the bulb is prepared for photography (**C, D**). S = scale, C = control mark.

sinkage of the substratum effects both control mark and bulb; therefore the distance to the control mark directly reflects any downward movement of the bulb.

Every 1–3 weeks each bulb was prepared and photographed (macro-lens Tamron 1 : 2.5, 90 mm, Olympus OM-2, stop-opening of f 16; Agfa-ortho ASA 25). A stand (GIZO, Gilux reporter) was used to maintain constant camera to bulb distance for each photo. After photographing, any cavities between the roots were carefully filled with substratum. The test containers were put together again and filled with substratum.

Results

Fig. 2 shows typical cryptocorms of *Nothoscordum inodorum*. When development begins the bulb (B) forms nutrient roots (NR). Subsequently contractile roots (CR) successively grow out. Morphological characteristics of root contraction are (1) expansion of diameter (in comparison to nutrient roots) and (2) shrinkage of root surface (sh in Fig. 2). Old nutrient roots may exhibit some shrinkage. However, bulb movement is not effected. Lateral bulbs (LB, daughter bulbs), which are useful for vegetative propagation, also forms nutrient (NR_L) and finally contractile roots (CR_L).

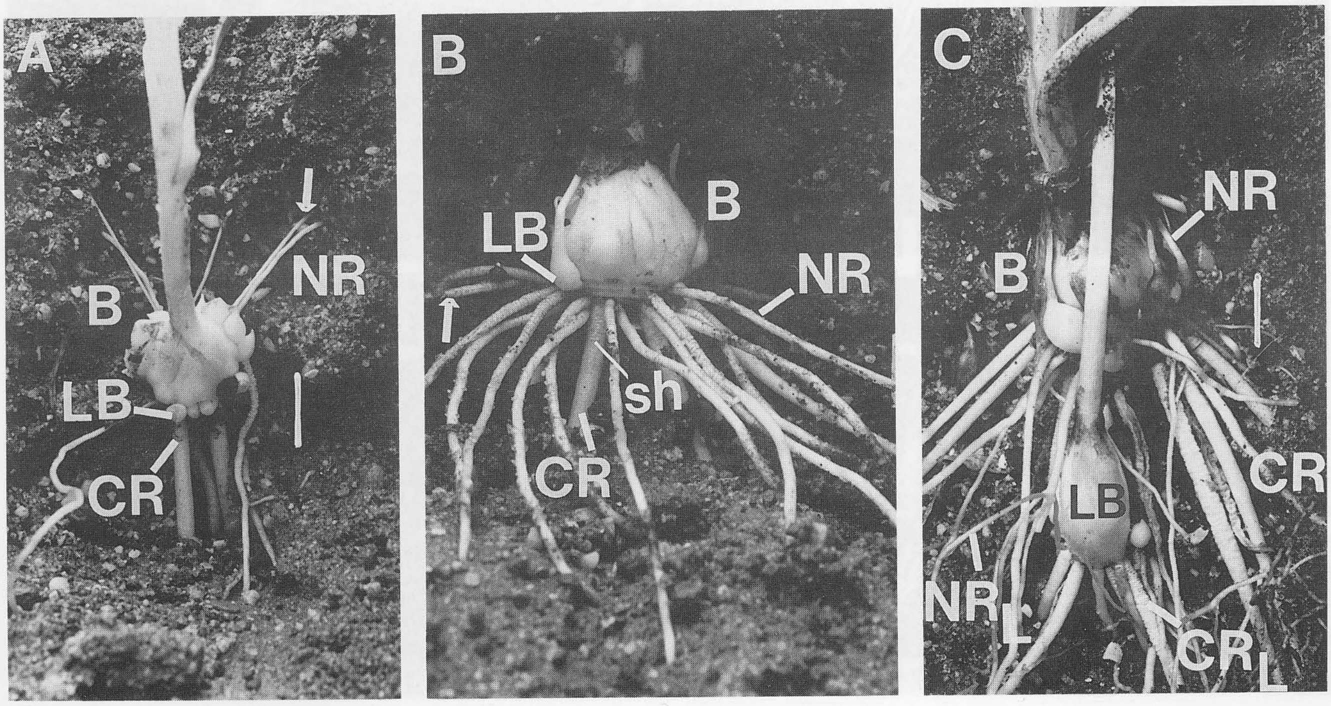

Fig. 2 Some cryptocorms of *Nothoscordum inodorum*. B = bulb, CR = contractile root (CR_L = contractile root of lateral bulb), LB = lateral bulb, NR = nutrient roots (NR_L = nutrient roots of lateral bulb), sh = shrinkage of root surface. Arrows show secondary change of the course of old roots caused by the continuous bulb movement.

Typical movement of the *Nothoscordum* bulb can be seen in Fig. 3. To demonstrate bulb to control mark position (C, resp. marked control line) the overall view of three stages are shown in Fig. 3 A. Bulb position to control line in Fig. 3 Ac demonstrates individual underground movement of approx. 40 mm. The other individual plants tested move between 30 and 50 mm.

In Fig. 3 B photos of 12 examinations of one individual plant are arranged as quick-motion pictures (date of examination is given in the lower section of each photo). Change in bulb position during the growing period is due to underground movement caused by the activity of contractile roots. Bulbs produce contractile roots successively, so that movement continues for approx. 40 weeks

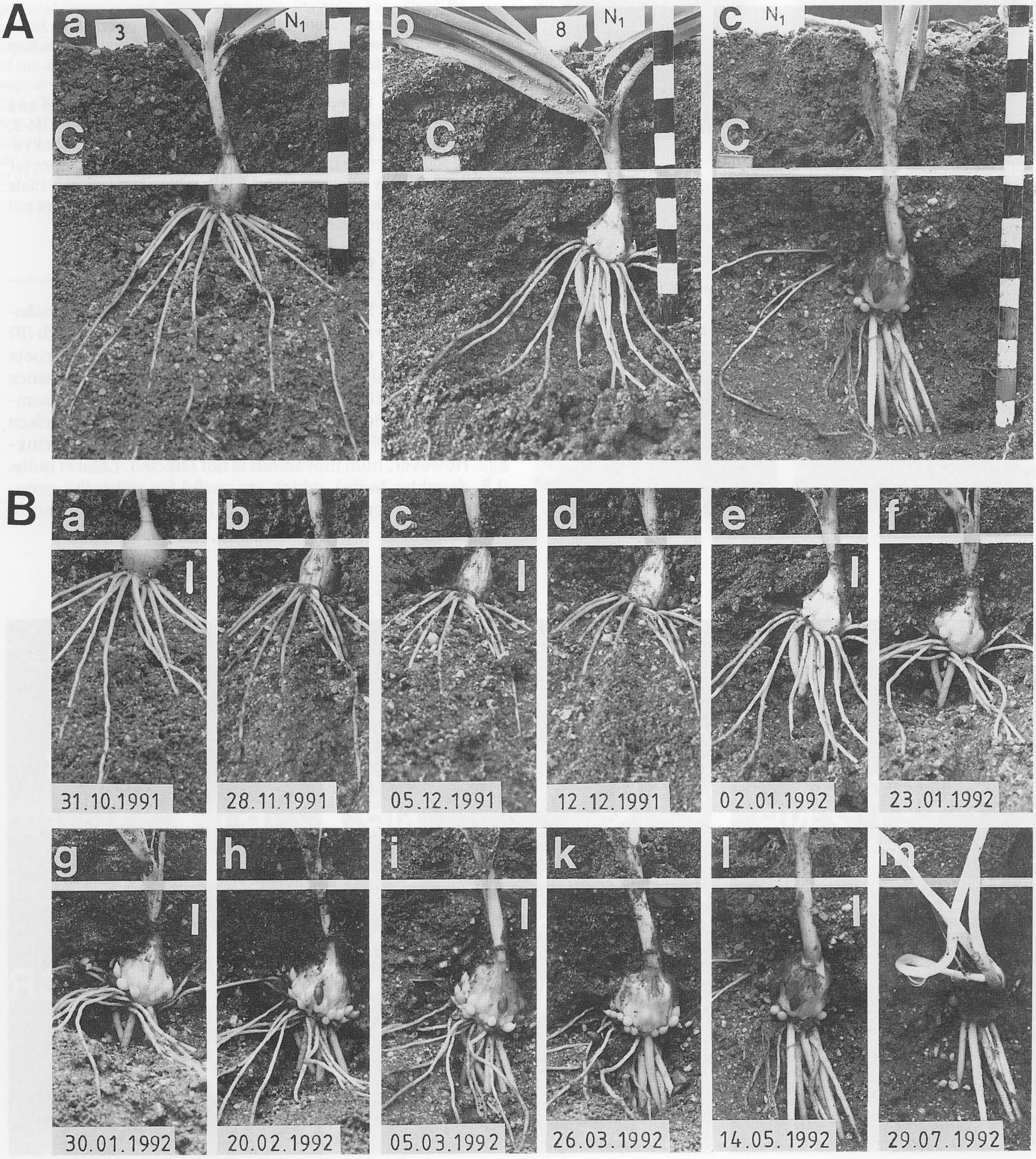

Fig. 3 Typical underground movement of *Nothoscordum inodorum*. **A:** Three stages of bulb movement to show the position of the bulb to the control line (resulting from the control mark, C). **B:** Bulb position of 12 examinations (date of examination is given in the lower part of each photo) shows movement as quick motion pictures. Bars represent 10 mm.

until the end of the growing period. Bulb diameter initially decreases (until Fig. **3 Bc**) but then increases considerably. The primary position of the bulb is upright. However, contractile roots chiefly grow out from one side of the bulb. Therefore root forces work on one side and result in a sloping position of the bulb (Fig. **3 Bd**, **Be**, compare Pütz, 1991, Fig. **5 E**). This movement can be described as tilting (Pütz, 1991). It is very important to note that the point of departure of new contractile roots changes slightly, so direction of tilt also changes. The individual plant in Fig. **3 B** first tilts over to the right but then increasingly to the front (Fig. **3 Bg–m**). So complete movement in the *Nothoscordum* bulb is not only tilting but twisting.

Normally, contraction of a single root takes about 50 days, maximum. Subsequently former contractile roots might adopt a nutritional function. However, the course of these old roots is deformed due to the continuous bulb movement. First it is curved (Fig. **2 B**, arrow). Finally it seems upright (nutrient roots in Fig. **2 A**, arrow).

Table **1** comprises the movements of the 15 tested objects. Only 6 individuals show a tilting movement. Complete movement has been observed in 6 of the 15 tested objects. However, tilting and twisting differs in direction, e.g. first to the left and then backwards etc. Three of the 15

Table 1 Direction of bulb movement of the 15 tested objects. The first column represents the number of individuals showing the same movement. Initial bulb movement is indicated by "1", change in direction is marked with "2".

number	right	left	front	back-wards	straight ahead
3	1		2		
1	1				
2		1	2		
1		1		2	
3				1	
2			1		
3					1

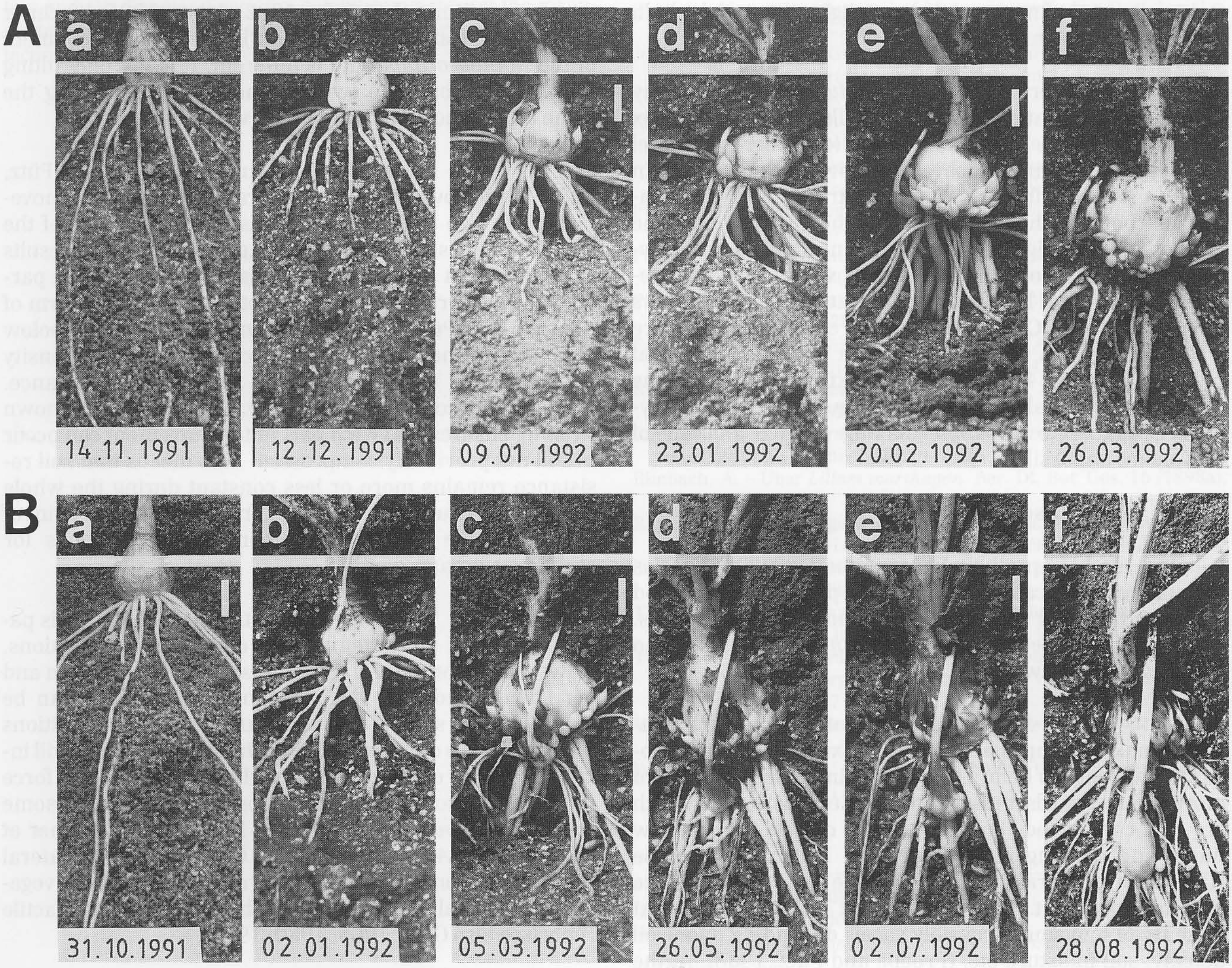

Fig. 4 Other possible movements of *Nothoscordum inodorum*.
A: straight ahead movement.
B: Separation of lateral bulbs.
White control line results from the control mark (C). Bars represent 10 mm.

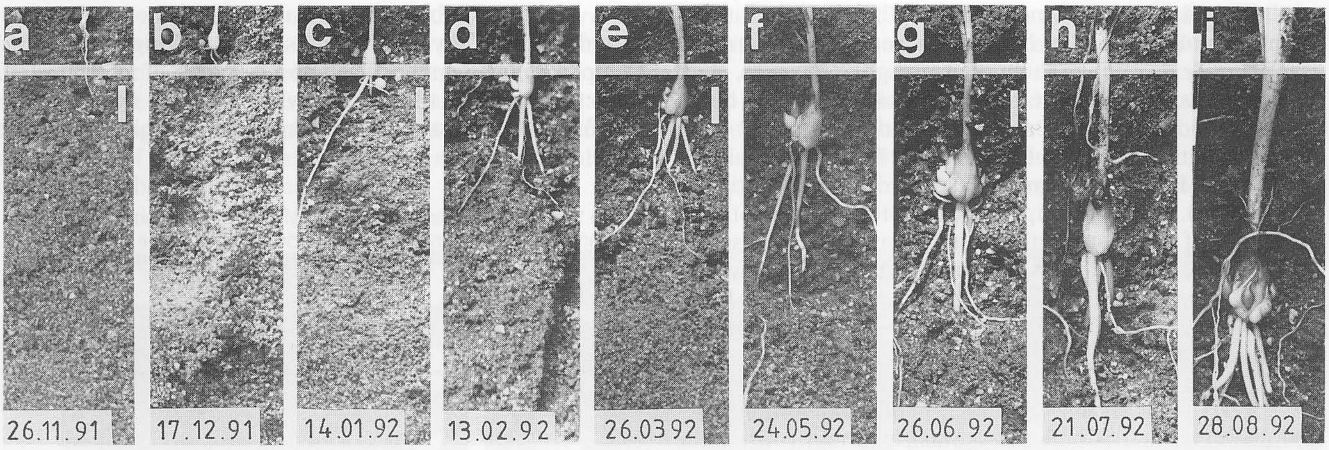

Fig. 5 Underground movement of *Nothoscordum* seedling as quick-motion pictures. Date of examination is given in the lower section of each photo. White control line results from the control mark (C). Bars represent 10 mm.

tested objects show an upright bulb position during downward movement. This is documented for one individual plant in Fig. **4A** (straight-ahead movement, Pütz, 1991). Only at the end of movement can a slight tilting of the bulb to the front be seen (Fig. **4Af**).

Very often *Nothoscordum* bulbs form many short petiolated lateral buds in a collateral bud complex (e.g. Fig. **2A**, **3Bh**). These lateral buds (daughter bulbs) peel off very easily during preparation. However, some remain on the mother bulb, form leaves, nutrient roots and contractile roots. In the second part of the growth phase the mother bulb in Fig. **4Bd–f** exhibits no movement. However, the activity of contractile roots still causes a movement of the lateral bulb, so that vegetative dispersal occurs (Fig. **4Bd–f**, Fig. **2C**). Growth and soil conditions used here lead to maximum distances between mother and lateral bulbs of approx. 40 mm. In the next growth phase the mother bulb and all lateral buds force and form a closely-packed aggregate of bulbs, making further analysis of movement impossible.

Discussion

In preliminary examinations some species reacted very critically to the special preparation method e.g. with necroses of the leaves or mortification of roots. However, most species, including *Nothoscordum*, show no disturbance of growth.

Re-filling the test container after preparation makes it impossible to reach exactly the same substratum density as before. This could influence direction of movement towards those parts of the substratum which are less compacted. Fortunately the objects tested show tilting and twisting in all directions. It can therefore be stated that preparation from one side does not affect the kind of movement. However, it must be mentioned, that quantity of movement possibly varies depending upon soil density, soil moisture etc. (Froebe and Pütz, 1988). At the same time movement of 30–50 mm as described here agrees well with experimental values using other techniques (35–41 mm, Pütz, 1993).

Nothoscordum bulbs exhibit two forms of downward movement. It can be supposed that straight-ahead movement occurs in many bulbous plants (see figures in e.g. Rimbach, 1898a, 1902; Arber, 1925; Kirchner et al., 1934; Dahlgren et al., 1985). The typical movement of the *Nothoscordum* bulb is different. It is not only tilting (Pütz, 1991), but also twists. Other species showing the same type of movement are unknown hitherto.

Preliminary experiments (Froebe and Pütz, 1988) have shown that various parameters influence movement, e.g. size of the bulb or moisture and density of the soil. Tilting is sometimes advantageous because it results in a movement which may take place in the direction parallel to the narrow end of the cryptocorm (e.g. the corm of *Arum* sp., see Pütz, 1991). During movement the soil below the bulb becomes more and more compressed. Soil density increases and this results in a higher soil resistance. Movement becomes more difficult. The hitherto unknown twisting ensures that each part of the movement can occur in soil not previously compressed. This means that soil resistance remains more or less constant during the whole movement. Thus it can be stated, from a functional point of view, that the twisting movement is advantageous for reaching a greater depth.

The direct observation described in this paper illustrates movement under optimal soil conditions. However, under natural conditions soil is non-uniform and very dense and thus soil resistance increases. It can be stated that the span of movement under natural conditions is lower. Twice during its lifetime the size of the bulb will increase. Since contractile roots show a maximum force (Pütz, 1992), soil resistance will become too high at some point and movement stops (Fig. **4B**, compare Kirchner et al., 1934; for *Agave americana*). Only the smaller lateral bulb retains some movement and demonstrates how vegetative dispersal is supported by the activity of contractile roots (see also Galil, 1965, 1980, 1983).

To reach an optimum depth, movement by contractile roots should begin at the seedling stage since the small seedling only has to overcome minimum soil resistance. In fact it is known that the primary root and first adventitious roots should be contractile (Rimbach, 1898a; Arber, 1925; Kirchner et al., 1934; Bussen, 1951; Tillich, 1992) and Jernstedt (1984) has observed downward movement with *Chlorogalum pomeridianum* seedlings of 63.8 ± 19.4 mm in a period of 29 weeks. Fig. **5** shows the movement of a *Nothoscordum* seedling. Several examinations of one individual plant have been arranged as quick-motion pictures. The first roots of *Nothoscordum* seedlings are contractile. Thus movement begins a few weeks after germination (Fig. **5 c**). The individual in Fig. **5** was able to move 74 mm over a 35 week period (movement of another 5 seedlings ranged from 65–85 mm, the average value is 75 ± 7 mm). Size of the young bulb increases during the growth phase and movement of the seedling becomes very similar to that of mature bulbs (Fig. **5 g–i**). Thus it can be said that movement of mature bulbs is part of an overall movement which starts with the seedling and enables the plant to reach optimum depth in the easiest possible manner.

Acknowledgements

I thank Mr. Leslie Cook for correcting the English text and Dr. Thomas Speck for helpful comments on the manuscript. I am very indebted to Mrs. Hana Akbari for preparation and technical assistance.

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N. Pütz

Botanisches Institut
Abteilung Morphologie
Rheinisch-Westfälische Technische Hochschule
52056 Aachen
Federal Republic of Germany