

Vegetative spreading of *Oxalis pes-caprae* (*Oxalidaceae*)*

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Abstract: The underground movement of *Oxalis pes-caprae* L. is a combination of shoot elongation and root contraction. Its function is the dispersal of renewal bulbs located in the axils of the scale leaves. At the beginning of root contraction the bulb leaves become detached from the bulb bottom and remain at their initial position. Bulb bottom and contractile root form a turnip-shaped unit. Its proximal end becomes displaced by shortening of the root. While contracting, the root develops a pulling force, which is quantified by using the lifting method. Connection between the overground shoot and the contractile root is maintained by a few short basal internodes of the new shoot, which elongate to form a thin underground “thread”. Elongation of the thread and shortening of the root reach 20–30 cm and obviously occur synchronously, whereby the thread remains taut during movement. Along the thread several lateral buds emerge. These develop into renewal bulbs usually reaching the size of the mother bulb.

The contraction of the thick fleshy roots of *Oxalis elegans* and *O. esculenta* was already described by RIMBACH (1895) and DUNCAN (1925), respectively. These authors supposed the roots to act as pull-roots causing a downward movement of the bulb. RIMBACH (1926) measured shortening up to 70% of parts of the root of various species of *Oxalis*.

In *Oxalis pes-caprae* L. the strong shortening leads to enormous vegetative spreading. GALIL (1968: 68) described two axes (1) “the vertical stem growing upwards” and (2) “a rootless horizontal thin stem” called “thread”. Vegetative dispersal takes place along with a horizontal succulent root: “As the root contracts the thread elongates, carrying along the tiny buds developed on it. In this way the buds are successively pulled out of the parent bulb and distributed along the now horizontal thread.” (GALIL 1968: 69). Thus an individual plant is able to distribute 10 (–40) bulbs along a distance of 20–30 (–47) cm.

However, details concerning the spreading process remained unknown. Firstly, information on the bulb structure and on its changes during the vegetation period

* Underground plant movement II. For first part see PÜTZ (1993).

is needed. GALIL (1968: 69) only said that “the thread elongates”. TROLL (1937–1943: 749) proposed the idea: “Die Zwiebeln der angeführten kapländischen *Oxalis*-Arten sind also vor allem dadurch merkwürdig, daß sie durch Internodienwachstum regelmäßig aufgelöst werden”. The same may apply to *Oxalis pes-caprae*.

Also the function of the succulent root is not really known. GALIL (1968: 68) suggests a pulling effect: the thread “is pulled by means of a large contractile root”. This means that the contractile root of *Oxalis* develops a pulling force during shortening. GALIL (1968: 69) also describes the succulent root and its relevance to the formation of underground soil channels: “The second part is the elongated thread extending horizontally within the tunnel vacated by the shrinking root”. But the growing axis may elongate in this tunnel without any root pulling.

The lifting-method (PÜTZ 1992a) makes it possible to measure the pulling force of a single contractile root. It is thus possible to get information about the activity of the succulent root of *Oxalis pes-caprae*. Therefore, both lifting-results and detailed structural analysis should help to provide a better understanding of the spreading process of *Oxalis pes-caprae*.

Material and methods

Plant material of *Oxalis pes-caprae* L. (*Oxalis cernua* THUNB.) was collected 1986 in Cinque Terre, Italy. From October to April the plants were cultivated in a green house, with minimum temperature varying from 14° C at night and 20° C during the day. 12 h daily the plants were illuminated with plant lamps (Osram, power star HQI-T 400 W/DH) to supply daylight. During summer the plants were stored under totally dry conditions at 20–25° C.

Quick-motion examination. 10 individuals were cultivated in special test containers made of PVC (40 × 40 × 20 cm) with one removable side-wall (compare PÜTZ 1993). This side-wall is fixed to the container by clamps. The containers were filled with a riddled sand/loam mixture and in each container one bulb was planted approximately 10 mm below the soil surface. 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 serving as a control mark (Fig. 1 A: C). Any sinkage of the substratum effects both control mark and bulb. Therefore the distance to the control mark reflects directly any downward movement of the bulb. Every 2–3 weeks each bulb was examined: the side-wall of the container was removed and the cryptocorm was carefully exposed (using a thin wooden stick and a brush), without removing the soil supporting the plant. After cleaning with a small jet of water (Primo disposable Syringes 20 ml and disposable needle 0,4 × 21 mm, hospital supplies) the object was photographed (macro-lens Tamron 1:2,5, 90 mm, Olympus OM-2, stop-opening of f 16, Agfa-ortho ASA 25). A tripod (GIZO, Gilux reporter) was used, maintaining constant camera distance to the bulb. After photographing any cavities between the roots were carefully filled with substratum. The test containers were put together again and filled with substratum.

Structural analysis. Different stages of development were prepared (Photomakroskop M 400, Wild, Heerbrugg) and photographed (Photoautomat MPS 55, Wild, Heerbrugg, see photo in Fig. 3 A).

Lifting-measurement. For detailed description of the method see PÜTZ (1992 a). 3 individuals were placed on stands (Fig. 5: ST) and cultivated in special culture chambers in a mist culture system. Activity of the roots was measured using the lifting-technique. Suitable roots were planted into small plastic tubes (100 mm length × 30 mm diameter, with bottom) located at the bottom of the culture chamber. The tubes were filled with substratum (a mixture of sand and loam) and therefore had a mass of approximately 90 g. Roots were fixed to the tubes using a “packing ring” of plaster of Paris to prevent pulling themselves

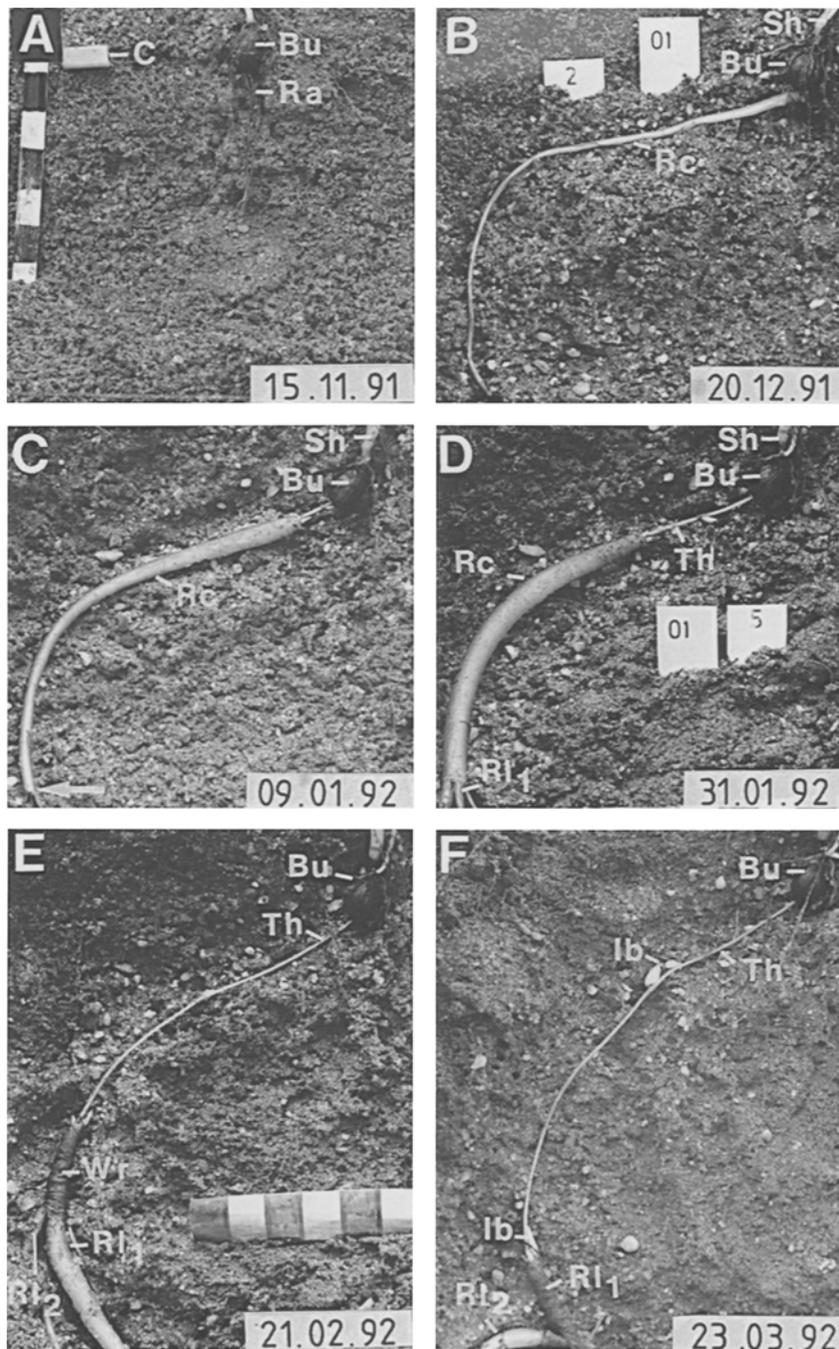


Fig. 1. *Oxalis pes-caprae*, A–F successive stages of the underground movement. Date of examination is given in the lower section of each photo. Root contraction is compensated by elongation of the “thread”. The arrow points to the damaged root tip. Bar: 10 mm. For abbreviations see Material and methods

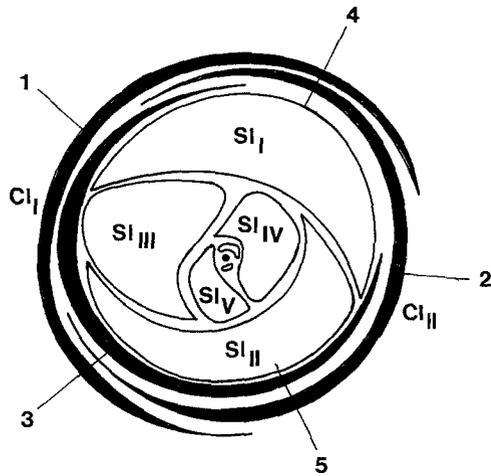


Fig. 2. *Oxalis pes-caprae*, schematic cross-section through a dormant renewal bulb. 1–5 numbering of the orthostiches. Black point in the centre represents the terminal bud. Further explanation in the text

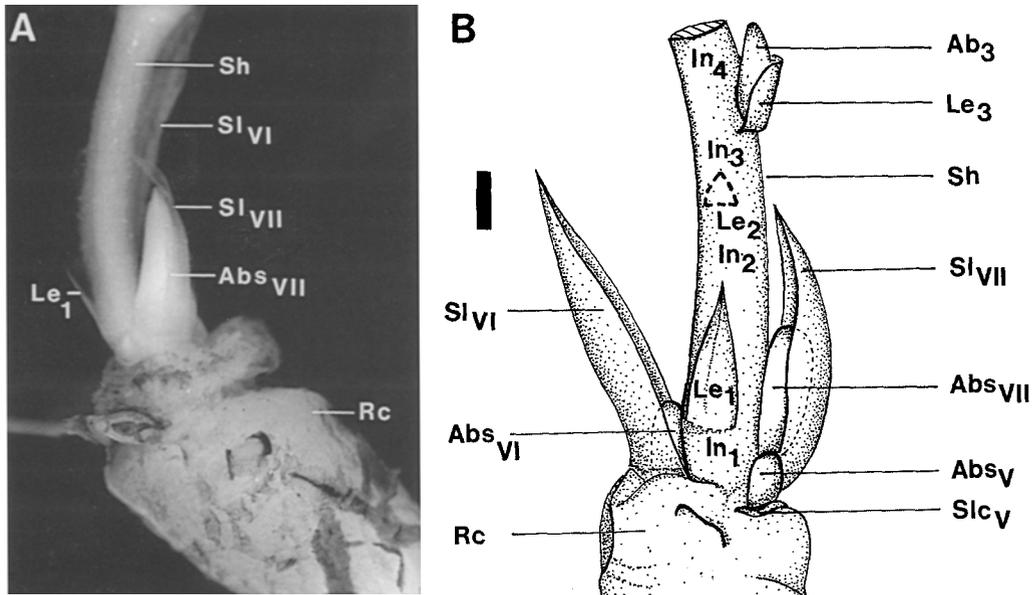


Fig. 3. *Oxalis pes-caprae*, inner bulb formation and base of contractile root before shortening in different views. All leaves removed except the two distal ones (Sl_{VI} and Sl_{VII}). Le₂ dotted, inserted on opposite side. Bar: 10 mm

out of the tubes when contracting. In previous measurements (PÜTZ 1992 a) the cryptocorm (bulb or corm) was fixed to the stand with coated wire. Thus, root force developed by root contraction results in lifting of the tube. Fixation of the *Oxalis pes-caprae* cryptocorm is not possible because of its elongation during the spreading process. Therefore, the root itself had to be fixed to the stand. This was carried out by clamping its proximal end with

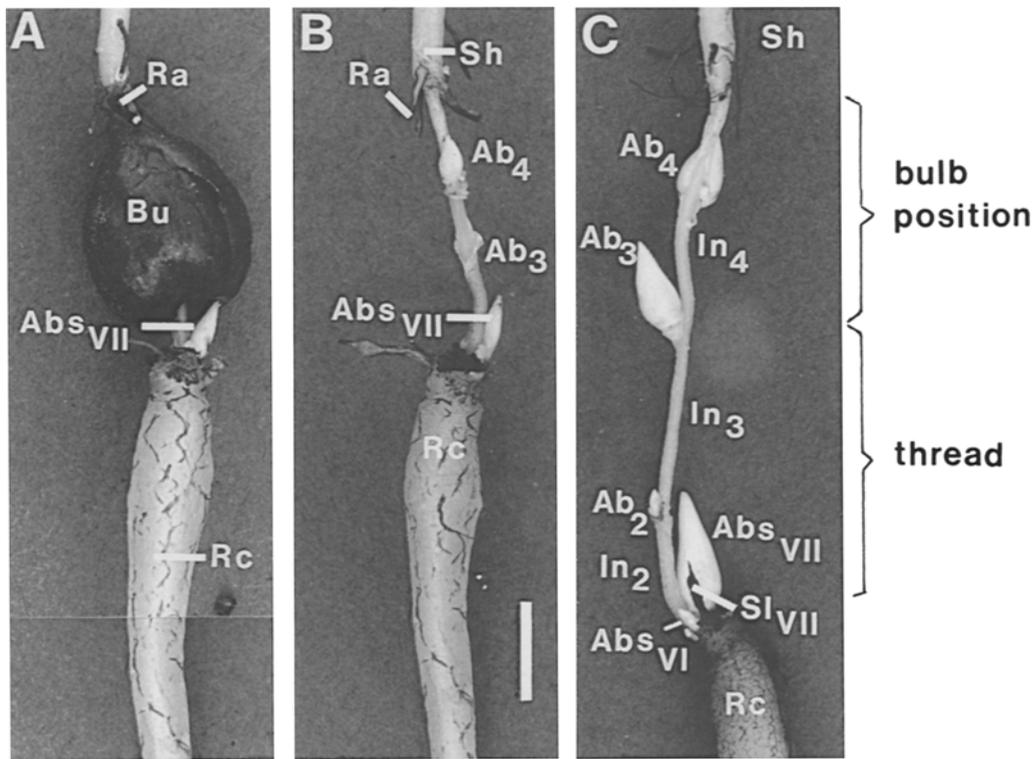


Fig. 4. *Oxalis pes-caprae*, cryptocorm at the beginning of root contraction and shoot elongation. *A* Specimen with mother bulb. *B* Same specimen without bulb scale. *C* Specimen in advanced shortening stage (position of bulb scale is shown on the right). In_1 and Le_1 cannot be seen at this magnification. Bar: 10 mm

a small vice (see Fig. 5). The occurrence and extent of root force were determined by measuring the change in distance (in mm) between the bottom of the tube and the bottom of the culture chamber during the course of an experiment. Measurement of the force of a single contractile root took about 35 d. There was no visible degeneration of the root due to clamping, packing ring, or culture conditions for at least six weeks.

Abbreviations used in text and figure. *Ab* axillary bud, *Abs* axillary bud of storage leaf, *Bb* bulb bottom, *Bs* bulb scale, *Bu* bulb, *C* control mark, *Cl* coat leaf, *Ib* lateral bulb, *In* internode, *Le* leaf of *Sh*, *Ra* adventitious root, *Rc* contractile root, *Rl* lateral roots, *Sh* shoot of the terminal bud, *Sl* storage leaf of the mother bulb, *Slc* scar of storage leaf, *Th* thread, *Tu* tube, *Vi* Vice, *Wr* wrinkling of the root surface. Roman numbers refer to organs of the mother bulb, arabic numbers to those of the new shoot (*Sh*).

Results

In Fig. 1 six stages of cryptocorm development of a selected plant are shown. At the beginning the bulb forms adventitious roots (Fig. 1 A: *Ra*) at its base as well as on the new shoot (*Sh*). Corresponding to the strong supply with nutritive substances and water the new shoot (*Sh*) quickly increases in diameter (Fig. 1 B). One (sometimes two) of the adventitious roots at the bulb base becomes fleshy, increasing

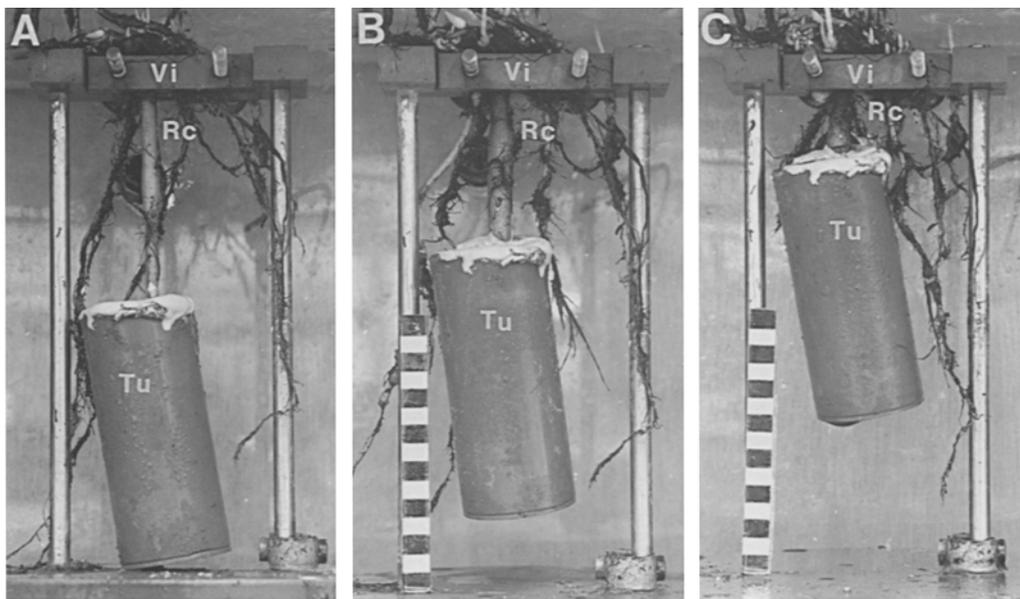


Fig. 5. *Oxalis pes-caprae*, lifting of a tube (90 g) by the contractile root. *A* Beginning of root contraction, the tube is lifted from the bottom of the culture chamber. *B* After 10 days, lifting distance: 20 mm. *C* After 22 days, lifting distance: 44 mm. Bar: 5 mm

in diameter up to 10–12 mm (Fig. 1 B, C). Subsequently the root shortens (Fig. 1 C–F). Especially in older roots the contraction is recognizable by wrinkling of the root surface (Fig. 1 E: *Wr*). Because of root contraction the mother bulb (*Bu*) is detached and remains at its initial position. The basal part of the new shoot, which GALIL (1968) called thread (Fig. 1 D–F: *Th*) elongates to the same extent as the root shortens. Under pot-culture conditions this elongation process reaches 20–30 cm (up to 42 cm), under natural conditions GALIL (1968) observed distances up to 47 cm. Along the thread several lateral buds (Fig. 1: *lb*) appear. These develop into daughter bulbs, finally reaching the size of the mother bulb.

Root shortening of up to 47 cm is only possible if the contraction process covers most regions of the root and is not – as usually in monocotyledons – limited to a few cm (RIMBACH 1926). Thus, the formerly 30–50 cm long root shortens to a shrivelled remnant of 5–10 cm located at the end of the thread (GALIL 1968).

Even if the root tip is damaged (as shown in the individual in Fig. 1, arrow) movement continues. At the damaged root tip several lateral roots appear and thicken (Fig. 1 D, E: *Rl*₁, *Rl*₂). Finally one of them (*Rl*₁) continues the contraction and thus the movement process. The second lateral root (Fig. 1 E, F: *Rl*₂) remains of no importance and becomes displaced by the activity of *Rl*₁.

The development of the mother bulb during the vegetation period gives information about the elongated part of the plant. A cross-section through a dormant bulb (diagram in Fig. 2) shows several leaves in 2/5 arrangement surrounding a terminal, undifferentiated bud. The outer scales (Fig. 2: *Cl*_{1–3}, black) form a hard “coat” (GALIL 1968: 69) to protect the inner parts of the bulb, e.g., from dryness. (5–)7(–9) ± succulent leaves (*Sl*_{I–VII}) store the nutritive substances for the next

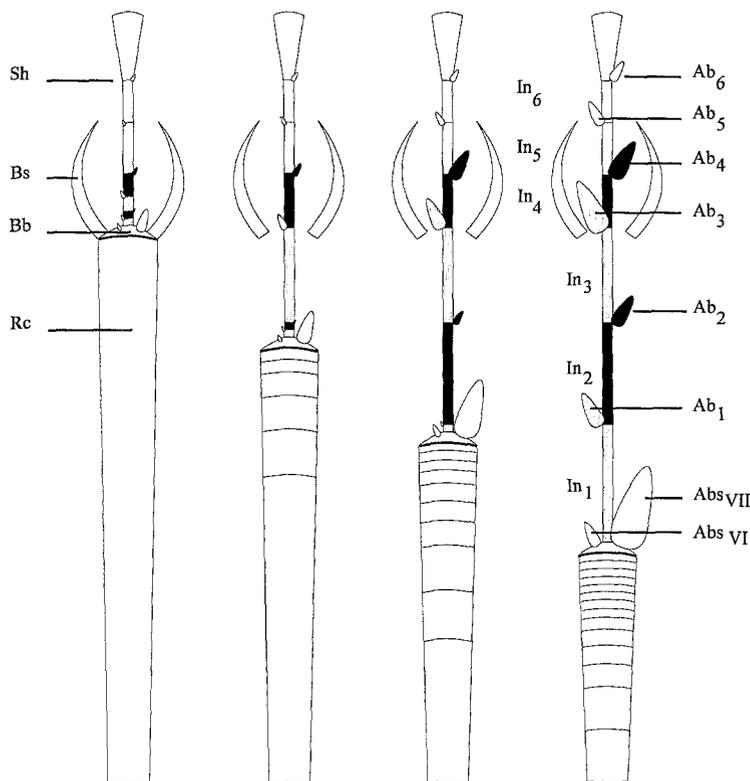


Fig. 6. *Oxalis pes-caprae*, schematic representation of the underground movement by root contraction and shoot elongation. The elongating internodes are coloured grey and black, leaves are not drawn. Cross lines on Rc symbolize advancing contraction

sprouting. Thickening of the inner storage leaves (Fig. 2: Sl_{VI} and Sl_{VII}) is only slight in comparison to the others. After the period of dormancy the bulb begins to sprout, forming an overground shoot, adventitious roots and a fleshy contractile root. In Fig. 3 A the bulb scales and the outer storage leaves have been removed to expose the bulb base. The proximal end of the contractile root (Rc) forms a unit with the bulb bottom (Bb). In the axil of the inner storage leaf (Sl_{VII}) there is a large axillary bud (Abs_{VII}). In Fig. 3 A the second storage leaf (Sl_{VI}) is mainly covered by the new shoot (Sh). Fig. 3 B therefore shows the same specimen from a different angle and it can be seen that Sl_{VI} has an axillary bud, too. This bud is very small in comparison to Abs_{VII} . It is clear that the axillary bud of the innermost storage leaf is advanced and, as it is the largest bud, is important for orientation in our study. The bud Abs_V in the foreground of Fig. 3 B is the axillary bud of the storage leaf Sl_V , the scar of which is visible at the base of the bud. It should be mentioned that axillary buds are present in all bulb leaves.

Next to the innermost storage leaf of the bulb (Sl_{VII}) the new shoot (Sh) grows up, at first bearing very small scales. In Fig. 3 A the first scale (Le_1) can be seen in side-view, in Fig. 3 B Le_1 can be found in top draw view, the following leaf (Le_2) is located at the back of the shoot (dotted lines). The next leaf (Le_3) is located on the same orthostiche as Sl_V or Abs_V and therefore clearly shows that the first leaves

of the new shoot continue the 2/5 phyllotaxis of the bulb leaves. The axillary bud Ab_3 of the leaf Le_3 is rather large, whereas those of the first leaves Le_1 and Le_2 are very small at this stage.

The internodes In_{1-4} below the first shoot leaves (Le_1 etc.) are very short. Therefore the scales Le_1 – Le_4 (– Le_6) and their buds remain within the bulb scale of the mother bulb (cf. Fig. 4). The next internodes (In_5 , In_6 etc.) become increasingly longer, so that the terminal bud reaches the soil surface and can develop into the overground shoot.

Figure 4 shows the start of movement. At the beginning of root contraction the bulb leaves become detached from the bulb bottom and remain in their initial position (Fig. 1). Bulb bottom and contractile root form a turnip-shaped unit, the proximal end of which becomes displaced by the shortening of the root. However, displacement is not transferred to the overground parts of the plant which is usual in most other species with depth regulation by contractile roots (e.g., RIMBACH 1898; PÜTZ 1991, 1993). After removing the old bulb scales a continuous axis can be seen, thickened above due to the plentiful supply from the nutrient roots (Fig. 4). Connection between the overground shoot and the contractile root is maintained by the elongating thread (GALIL 1968). This thread corresponds to the new shoot. For orientation, the largest bud in Fig. 4 is the axillary bud of the innermost storage leaf (Abs_{VII} of Sl_{VII}). According to Fig. 3 there are at least 4 nodes and internodes of the shoot (In_{1-4} of Sh) within the bulb scale. However, in Fig. 4 B only two nodes with their leaves and buds can be seen. These leaves must be Le_3 and Le_4 , their buds being Ab_3 and Ab_4 , and their internodes In_3 and In_4 . This can be ascertained with reference to Fig. 4 C, which shows a specimen with advanced elongation. Due to the root activity the bud Abs_{VII} moves downwards. The buds Ab_3 and Ab_4 still remain within the old bulb scale (the position of the scales is marked on the right of Fig. 4 C). The internode In_4 lying between the buds shows only little elongation, but the internodes In_3 and In_2 show a strong elongation so that the scale Le_2 and its very small axillary bud Ab_2 become visible in Fig. 4 C. Further elongation of the thread includes the internode In_1 , so that Le_1 finally appears at the thread, too. Very strong elongation may effect some of the internodes of the mother bulb and the buds Abs_{VII} and Abs_{VI} appear on the thread. Normally, however, elongation is limited to the first 4 internodes of the new shoot.

To locate the main activity of elongation a thread was punctuated with a "Baumschulmarker" (edding 8070). Examination after ten days showed continuation of the movement process of several centimetres. However, the marked points remained in the initial position, elongation of the thread thus occurred only near to the contractile root.

Several of the axillary buds develop into bulbs, thus renewing the system in the next vegetation period. The bud of the innermost storage leaf Sl_{VII} is advanced and in stunted plants is the only one to develop. In most cases the buds Abs_{VI} , Abs_{VII} and Ab_{1-4} grow up to renewal bulbs, Ab_3 and Ab_4 normally being located within the still existing bulb scales of the mother plant. In addition, several buds at the base of the shoot (e.g., Ab_5 , Ab_6 etc.) may develop into bulbs. At the end of a growing period 8–10 renewal bulbs can be found along the thread. In very vigorous plants GALIL (1968) counted up to 40 new bulbs, apparently having developed from buds at the shoot base and the bulb bottom.

Elongation of the thread and shortening of the root obviously occurs synchronously, whereby the thread remains taut during movement. Some lifting measurements have been carried out to check whether root shortening results in a force which determines the direction of spreading. The three tested roots lifted the 90 g tubes off the bottom, thus demonstrating the considerable pulling force developed during contraction. Two of the measurements had to be stopped at a lifted distance of 7 resp. 9 mm, because anchorage of the cryptocorm was insufficient. The third measurement was successfully completed and thus provided an important indication of the dimension of root force and power. Fig. 5 A–C demonstrates the lifting process of the tube by photographs. At the beginning the tube was standing at the bottom of the culture chamber. Lifting started after three days (Fig. 5 A). After 10 days the tube was lifted about 20 mm (Fig. 5 B), and after 22 days the lifting distance to the bottom of the culture chamber reached 44 mm (Fig. 5 C). Lifting movement stopped at 49 mm after 28 days. Calculation (see PÜTZ 1992 a: 1437) yields a pulling force of approximately 0.9 N, work equal to 0.043 J and power equal to $1,8 \times 10^{-8}$ W.

Discussion

MARLOTH (1907: 319) interpreted the function of the sap roots of *Oxalis pes-caprae* as a temporary water storage organ: “. . . während das in ihnen gespeicherte Wasser und die vorhandenen Nährstoffe zum Ausbau der neuen Zwiebelchen verwendet werden, welche den Sommer zu überdauern haben.” A similar idea was proposed by DUCELLIER (1914). Experiments with $^{14}\text{CO}_2$ and ^{14}C in *Oxalis bowieana* (IZIRO & HORI 1983 c) corroborate this hypothesis.

In his eco-morphological study GALIL (1968) described another function of the contractile root regarding its importance as an organ of movement and provided important information about orientation of the root depending on depth and external conditions. However, structural details are still largely unknown. TROLL (1937–1943), when dealing with some other South-African *Oxalis* species, focused on the phenomenon of the regularly bulb decease and, in principle, detected an important aspect of the movement complex.

Spreading movement of *Oxalis pes-caprae* is characterized both by elongation of the shoot and contraction of the root. Typical behaviour is schematically represented in Fig. 6. The first internodes of the new shoot (Sh) are very short (Fig. 6 A) but elongate successively during the movement process (see Fig. 6 A–D). The second important part of the movement is the contractile root, the force of which determines the direction of elongation and at the same time forms a channel or tunnel in the soil for the following thread (“pioneer-root”, GALIL 1980, “Kanaleffekt”, FROEBE & PÜTZ 1988). Measurements were carried out here for the first time and give the quantitative dimensions of force, work, and power of a dicotyledonous contractile root. The pulling force of many monocotyledons such as *Sauromatum guttatum* (0,008 J, PÜTZ 1992 a) amount only to the fifth of the work of an *Oxalis* contractile root. Only species with a root diameter of at least 10 mm and a big channel effect have powerful roots and show comparable values (e.g., *Tigridia pavonia*: 0,048 J, PÜTZ 1992 b). It seems that root diameter provides a yardstick for evaluating the force of a given contractile root. Root force does not seem to depend on the various anatomical mechanisms of root contraction. In contrast to most monocotyledons

the anatomical mechanism of *Oxalis pes-caprae* is characterized by a special stage-like collapse of the cortical cells (see ROHDE 1928, THODAY 1926, THODAY & DAVEY 1932). However, detailed information on anatomical changes during contraction and on the physiological process necessary for building up a root force is still lacking.

It is known that internodes may first remain short but later elongate by the activity of intercalary meristems. Normally, the direction of elongation is determined by external conditions, e.g., gravitation. It is interesting that in *Oxalis pes-caprae* the growth direction of the root and its force determine the direction of internode elongation. GALIL (1968) reports that sometimes the thread is not freed from the mother bulb. In these cases, root force works on the entire mother plant and "the thread becomes coiled inside the bulb" (GALIL 1968).

The total movement process — shoot elongation combined with root contraction — results in a very effective dispersal of the renewal bulbs. From an ecological point of view it is also significant that external conditions may influence the induction and orientation of contractile roots. Unfortunately, little is known about induction of contractile roots (GALIL 1958, JACOBY & HALEVY 1970, HALEVY 1986). The dealing with *Oxalis* species (GALIL 1968; IZIRO & HORI 1983 a, 1983 b) point out several adaptations of vegetative dispersal to external conditions. Obviously *Oxalis* is able to react to planting depth or light/shadow with different orientation of its contractile root. Thus depth of the renewal bulbs is adapted to their actual location. Spreading can be directed downwards, though horizontal orientation of the root is also possible and ought to be common (GALIL 1968).

In summary, it can be said that *Oxalis pes-caprae* exhibits a very particular underground movement that results in an enormous vegetative propagation. Despite the lack of seed production (GALIL 1968) it is not surprising that this South-African species is well-established in the Mediterranean area.

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