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Comparative examination of the moving process in monocot and dicot seedlings using the example *Lapeirousia laxa* (Iridaceae) and *Foeniculum vulgare* (Apiaceae)*

With 4 Figures

Summary

Geophytes require a special depth in the soil, and therefore, seedlings of many plant species move downward very soon after germination. In this paper, a comparison is made using two examples, the mono-cotyledonous *Lapeirousia laxa* and the dicotyledonous *Foeniculum vulgare*. Using time lapse photography, functional differences become clear, characterised by typical seedling morphology.

During germination of *Foeniculum vulgare*, the hypocotyl elongates, which later has to be compensated by root and hypocotyl contraction in order to give the perennation buds a lower position for sprouting in the following year. In *Lapeirousia laxa* the primary internodes remain short, and form the perennation organ (a corm), with their perennation buds protected by soil from the outset. Downward movement of the corm occurs by the contractile roots which develop successively at the corm. At the end of the first vege-tation period, the corms of *Lapeirousia laxa* are in a 60–100 mm deeper position. In contrast, *Foeniculum vulgare* develops a turnip as its perennation organ, which, through self-contraction causes the perennation zone to become lower. At the end of movement, the perennation buds are approximately 15–25 mm below the soil surface, while the total movement of the buds is measured to be 30–40 mm.

Zusammenfassung

Geophyten benötigen eine spezielle Tiefenlage im Boden, so daß schon ihre Sämlinge bestrebt sind, möglichst rasch in das Substrat einzudringen. Der exemplarische Vergleich zwischen einer Monokotylen *(Lapeirousia laxa)* und einer Dikotylen *(Foeniculum vulgare)* mit Hilfe direkter Bewegungsanalysen läßt funktionelle Unterschiede erkennen, die geprägt sind durch den morphologischen Bau der Keim-linge.

In der ersten Keimungsphase wird bei *Foeniculum vulgare* eine Hypokotylstreckung deutlich, die nach-folgend durch Kontraktionsprozesse wieder ausge-glichen werden muß. Dadurch sinken die Innova-tionsknospen auf Erdniveau und sind bereit für den nächstjährigen Austrieb. Bei *Lapeirousia laxa* blei-ben dagegen die Internodien der Primärachse sehr kurz und bilden schließlich als Überdauerungsorgan eine Rhizomknolle aus, deren Innovationsknospen zu jeder Zeit von Substrat geschützt sind. Die Be-wegung erfolgt durch Zugwurzeln, die sich suk-zessiv an der kurzen Sproßachse entwickeln, und die Knolle erreicht schließlich Bodentiefen von 60–100 mm. Bei *Foeniculum vulgare* ist dagegen das Überdauerungsorgan Rübe selbst durch ihre Kon-traktion für die Abwärtsverlagerung ihrer Innova-tionszone verantwortlich. Der Rübenkopf mit seiner Innovationszone befindet sich schließlich etwa 15–25 mm unter der Erdoberfläche; bei einer gemesse-nen Gesamtbewegung durch Rübenkontraktion von 30–40 mm.

Introduction

Seedlings of many geophytes in the monocotyledons show extensive underground movement, caused by the activity of contractile roots (e. g., RIMBACH 1897a; JERNSTEDT 1984). Information can be obtained directly by time lapse photography, e.g., of the seedlings of *Nothoscordum inodorum* (PÜTZ 1993) and *Sauromatum guttatum* (PÜTZ 1996).

In dicotyledonous seedlings the principle of underground movement caused by root contraction is also known (TROLL 1937–1943). Several reports, for example, about the seedling of Apiaceae *Foeniculum vulgare* are available (RIMBACH 1921; TROLL 1937–1943; BRUCH 1953), including the phenomenon of contraction: "Bereits zur Zeit der Entfaltung des zweiten bis dritten Primärblattes setzt eine charakteristische Längskontraktion der Primärwurzel ein, welche bewirkt, daß die Sproßachse in die Erde gezogen wird. Damit ist ein Schutz gegen die Gefahr des Auswinterns geboten. Die Kontraktionserscheinungen, die später auch auf das Hypokotyl übergreifen, äußern sich durch auffallende Querrunzelung" (BRUCH 1953: 4). However, time lapse photography (PÜTZ l.c.) of dicot seedlings are not currently available. Preliminary examinations have been successful, in particular with *Foeniculum* seedlings. A description of this species seems useful in establishing to what extent our functional anylysis could add new and interesting facts in connection with such a 'well-known phenomenon'.

Furthermore, we examined the seedling movement of another monocotyledonous plant, the Iridacee *Lapeirousia laxa*. Thus, we were able to compare the typical movement of a monocot geophyte with the typical behaviour of a dicot turnip geophyte. Even the primary morphological organisation of the seedlings shows distinct differences (e.g., Fig. 1 in TILLICH 1992), which definitely produces characteristic features of the functional moving process.

Material and methods

Seeds of *Lapeirousia laxa* (THUNB.) N.E.BR. (Iridaceae) and *Foeniculum vulgare* subsp. *vulgare* var. *dulce* (MILL.) THELL. (Apiaceae) were obtained from the Botanical Garden of the Rheinisch-Westfälische Technische Hochschule (R.W.T.H.) Aachen. Examination took place in special test containers (∅ 25 cm, 10 l), which had removeable side walls. Thus, the individual plant could be dug out and photographed from the side (details of the examination method are described in PÜTZ 1993). This was repeated in 1–2 week intervals and thus, sequences of time lapse photographs could be compiled.

The test containers were filled with riddled sand/loam mixture (according to FROEBE & PÜTZ 1988). Five seeds were placed at a distance of 3 cm from each other. An aluminium control mark was located next to the seeds. The distance from the seedling to this control mark (drawn as white dotted lines in the Figs. 2 and 3) measures its underground movement. The seeds were covered with 5 mm of soil. Up to the start of germination, the pots were covered with glass-plates to stop the soil from drying, and were placed in the greenhouse of the Botanical Institute of the R.W.T.H. Aachen. Ten pots were prepared for each species. Cultivation took place at a minimum temperature of 15 °C at night and 20 °C during the day. Plants were illuminated with plant lamps (Osram, power star HQI 400 W/DH) for 12 h daily as a supplementary source of illumination to daylight.

Results

A typical monocot and a typical dicot seedling have some common features, but show also some important differences (compare Fig. 1 in TILLICH 1992: 93). *Lapeirousia laxa* and *Foeniculum vulgare* represent such typical seedlings, and in our functionally oriented investigations two structural features are especially important (Fig. 1):

1. The hypocotyl elongates in *Foeniculum vulgare* up to several centimeters (3–5 cm), whereas in *Lapeirousia laxa* the internodes of the shoot remain very short (the hypocotyl in *L. laxa* elongates up to 1–2 mm).
2. Radication in *Foeniculum vulgare* is allorhizal. However, the radicle in *Lapeirousia laxa* very soon becomes supported by adventitious roots (see BUSSEN 1951) and the radicle finally disappears (adventitious root system, homorhizal).

Thus, the initial conditions contrast greatly, and it is not surprising that downward movement in both species has characteristically distinctive features.

Foeniculum vulgare

Time lapse photography in Fig. 2 shows that downward movement and development of the
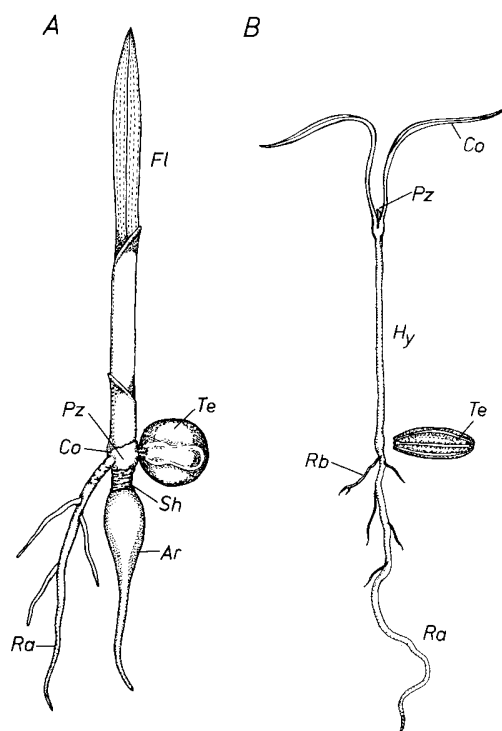
Fig. 1
Seedlings of *Lapeirousia laxa* (A) and *Foeniculum vulgare* (B)

Ar – adventitious root; Co – cotyledon; Fl – foliage leaf; Hy – hypocotyl; Pz – perennation zone; Ra – radicle; Rb – boundary root (Grenzwurzel); Sh – shrinkage; Te – testa

30 days (Fig. 2C). The cotyledons are pulled downward by shortening of the radicle and hypocotyl and become closer to the soil surface. Wrinkling of the surface increases during this contractile process. The cotyledons now degenerate, but their attachment and their axillary buds reach the soil surface due to continuous contraction (Fig. 2D).

Epicotyl and some other internodes remain short, and thus the first foliage leaves develop just above the cotyledons (see Fig. 2B), creating a leaf rosette at the tip of the growing turnip. The axillary buds of the rosette leaves are important as a perennation zone after dormancy, and continuous shortening causes this leaf rosette to move into the soil (Fig. 2D–F) to reach a safe position. Thickening of hypocotyl and radicle is necessary for storage, and combined with the resting buds, the turnip constitutes as a perennation organ for sprouting after dormancy. The perennation zone at the tip of the turnip reaches a 15 mm deeper soil position (Fig. 2G) in comparison with the starting position of the seed (Fig. 2A, dotted line). However, in other tested individual plants the perennation zone reached a depth of up to 25 mm.

Lapeirousia laxa

The shoot (axis) remains very short, as does the cotyledon (compare Fig. 1B). Thus, the following cataphylls (primary leaves) are the first leaves to assimilate. The corm, being the perennation organ for dormancy, remains very small during the first stage of development (Fig. 3A–E). However, it finally reaches a size of 10–15 mm. At this time (Fig. 3H, I, after 6 months) the corm becomes positioned approximately 90 mm deeper in the soil than the original position of the seed (Fig. 3A), and therefore can survive in safety. In our investigations depth ranges from 60–100 mm in the other tested individual plants. The force behind movement originates in the adventitious roots, which appear successively at the corm. These roots first show strong swelling, after which the surface wrinkles. This is characteristic of root contraction (Fig. 3E, H). The radicle only shows slight wrinkling, and thus has only low pulling force (Fig. 1). In the first phase of development the plant body is very small and can be moved without greater expenditure of energy, and this is when root pulling
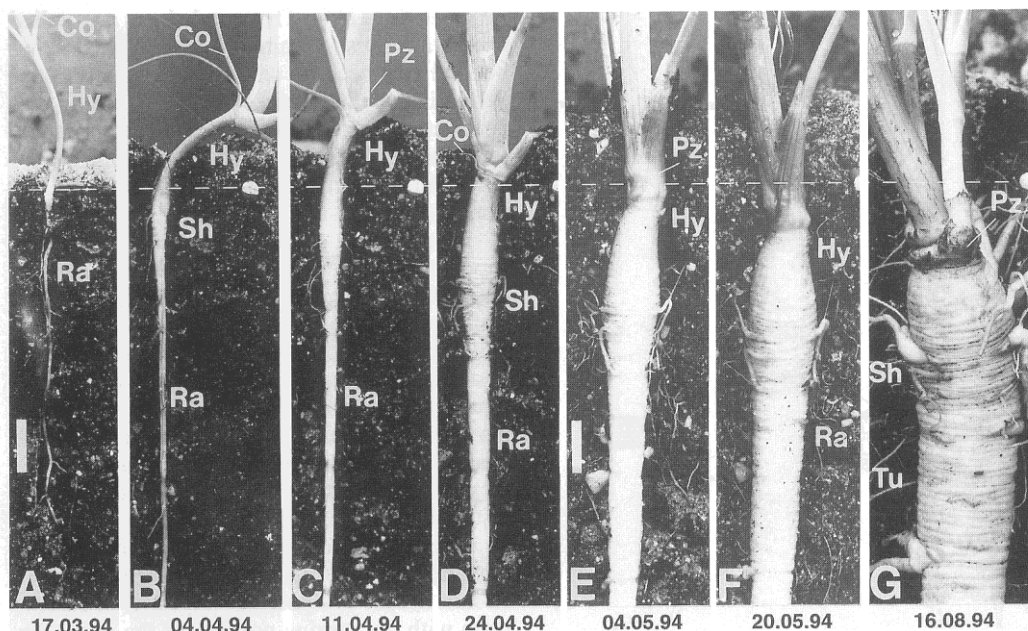
perennation organ (here: the turnip) occurs synchronously. After germination, the radicle penetrates downward into the soil, whereas the hypocotyl elongates upward. After elongation of the hypocotyl, the two cotyledons become positioned approx. 35 mm above the soil surface and function for photosynthesis (Fig. 2A). According to BRUCH (1953), the boundary between radicle and hypocotyl, the root neck (Wurzelhals), is defined by the first lateral root, the boundary root. During development, a thickening of both, radicle and hypocotyl appears. At the same time, the radicle shows the first wrinkles on its surface (Fig. 2B), which are a characteristic feature of root contraction. The hypocotyl also becomes much shorter (from approx. 35 mm in Fig. 2A to 27 mm in Fig. 2B and only 20 mm in Fig. 2C). However, first wrinkles appear after approx.

Fig. 2

Foeniculum vulgare: underground movement of a seedling as time lapse photography. Date of examination is given in the lower section of each photo. The control marks are shown as a white dotted line. Bars represent 10 mm.

Co – cotyledon; Hy – hypocotyl; Pz – perennation zone; Ra – radicle; Sh – shrinkage; Tu – turnip

produces a comparatively quick downward movement (Fig. 3B to G, in 12 weeks approx. 66 mm). The position of the old, contracted roots becomes changed by the continuous movement of the corm. Thus, the older roots bend and finally become upright (arrows in Fig. 3E, F).

Discussion

Bulbs, corms or turnips are perennation organs which carry out storage and innovation functions. Storing differs from species to species and may occur in stem, root or leaf. However, innovation, with the exception of the special case of root suckers, is limited to the shoot buds only. In *Lapeirousia laxa* and in most monocotyledons, the first internodes of the axis remains very short (TILLICH 1992), and after germination the primary position of the perennation zone of the

following year is below the soil surface. Furthermore, many monocots elongate the base of their cotyledon (e.g., RIMBACH 1897a for *Allium ursinum*; RIMBACH 1897b for *Colchicum autumnale*; RIMBACH 1928 for *Zantedeschia aethiopica*; WOODHEAD 1904 for *Scilla festalis*; GALIL 1983 for *Ixiolirion tataricum*), and thus, push the very short primary axis downward by a few millimeters. In *Pancratium maritimum* L.[1] in Fig. 4A, for example, the short axis, at this stage still covered by the cotyledon, is pushed downward by approximately 22–25 mm. Subsequently, adventitious roots take over this downward movement by virtue of their pulling force (contractile roots, compare Fig. 4B).

In the seedling of *Foeniculum vulgare* the first chance for buds to perennate in the next vegetation period is constituted by cotyledonar buds. These buds are positioned few centimeters above ground, due to hypocotyl elongation, which is quite common in dicotyledons. However, in the case of perennation, a change in the position of these buds is necessary and a move-
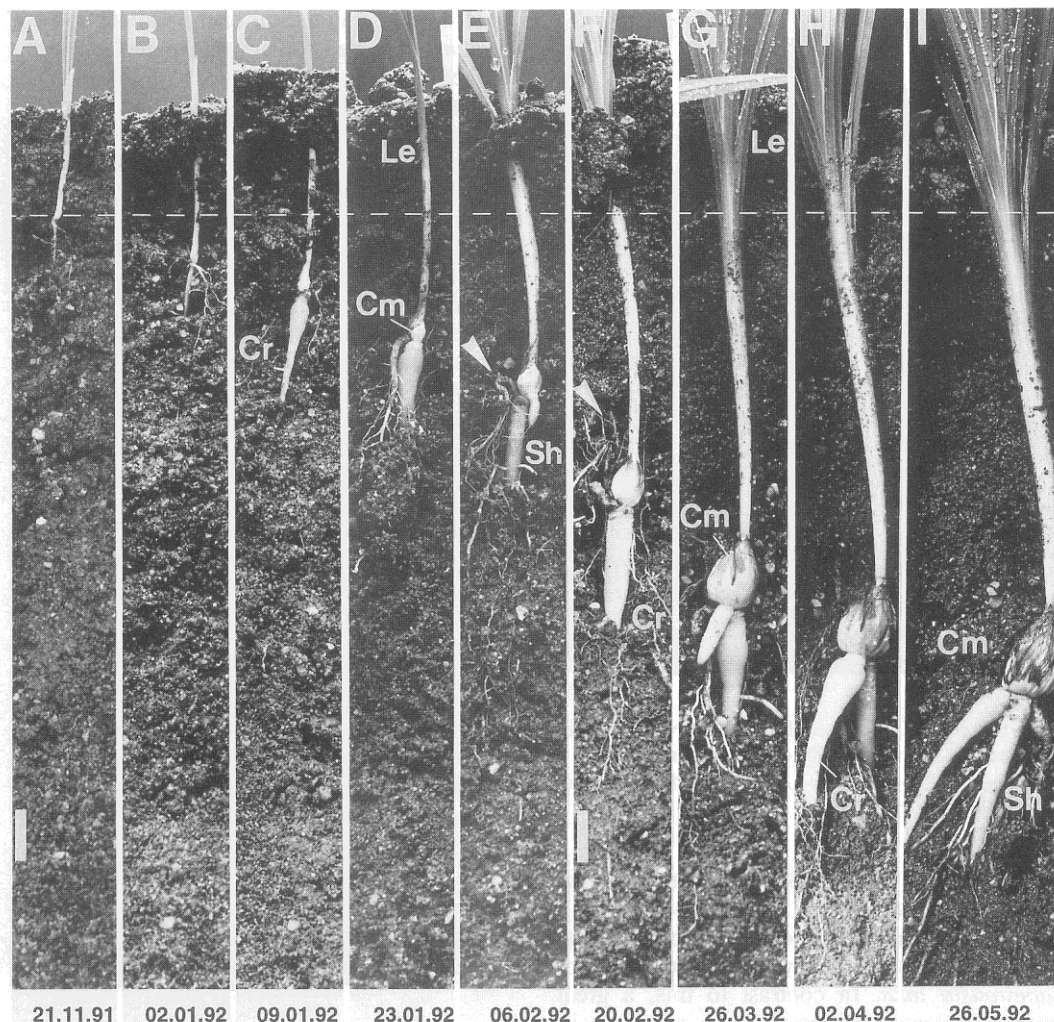
Fig. 3
Lapeirousia laxa: underground movement of a seedling as time lapse photography. Date of examination is given in the lower section of each photo. The control marks are shown as a white dotted line. Bars represent 10 mm.
Cr – contractile root, Cm – corm, Le – leaf, Sh – shrinkage. The arrows show the secondary position of older roots.

ment occurs, which is above ground in the first phase, and continues in the soil. Measured by cotyledons attachment in Fig. 2A, the total movement of the perennation zone of the individual shown reaches approximately 40 mm, caused by contraction of root and hypocotyl. In some other dicot species having turnips we found a total movement of approx. 35 mm (*Cichorium intybus,* Asteraceae) and 30 mm (*Daucus carota,* Apiaceae). The channel effect, which is 100% in

turnips (FROEBE & PÜTZ 1988; PÜTZ et al. 1995), ensures that there is no energy loss to overcome soil resistance during the moving process. Although some further investigations remain to be carried out with dicot species it seems clear, that the total extent of movement in dicot turnips is smaller than the monocot seedling movement. In monocot, measured movements were of the order of 60–100 mm: *Chlorogalum pomeridianum* (JERNSTEDT 1984: 63.8 ± 19.4 mm); *Nothoscor-*
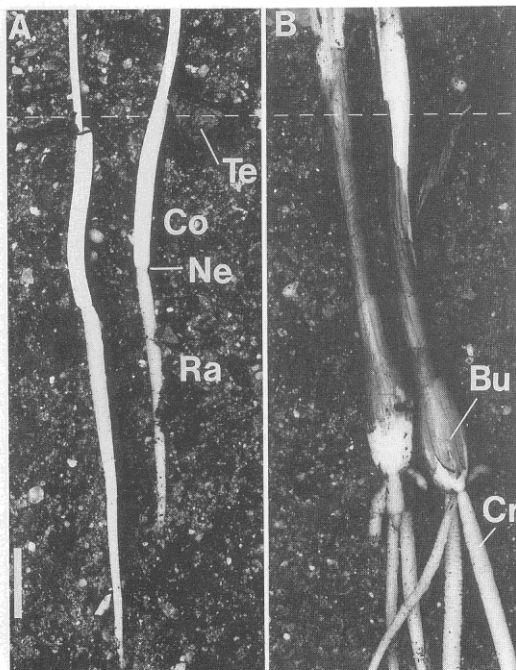
Fig. 4
Pancratium maritimum seedlings: (A) five days after germination, (B) same individual after 5 months

Bu – bulb, Co – cotyledon, Cr – contractile root, Ne – root neck, Ra – radicle, Te – testa

dum inodorum (PÜTZ 1993: 75 $\pm$ 7 mm); *Sauromatum guttatum* (PÜTZ 1996: 70–100 mm). Furthermore, monocot species can be found at these depths, as can easily be seen in Fig. 3 for *Lapeirousia laxa*. In contrast to this, a great amount of downward movement is necessary in turnips to compensate for the hypocotyl elongation in the first germination phase, and in normal cases the perennation zone of the turnip is located at a soil depth of approx. 10–25 mm (e.g., DE VRIES 1880 for *Trifolium pratense*; TROLL 1937–1943 for *Gentiana lutea*; STEIN & WEBERLING 1992 for *Acaena cylindristachya*).

With monocotyledonous geophytes such as *Lapeirousia laxa* there is a clear separation between the force of movement (contractile adventitious roots) and perennation (bulb or corm). In contrast, dicot turnips do not have a comparable separation. The perennation organ (turnip) also has to carry out bud movement and is only able to do so, because both radicle and hypocotyl have a strong ability to contract.

However, contraction of the radicle in *Foeniculum vulgare* and other turnip plants may have another function. In this context, observations of aerial roots of some dicot wooden plants provide pointers. The aerial roots of *Coussapoa schottii*, Urticaceae (NORDHAUSEN 1913) or *Ficus benjamina,* Moraceae (ZIMMERMANN et al. 1968) show extensive contraction, and therefore, become tensioned between the soil and the stem of the plant. Thus, the roots function like safetying ropes and appear to be useful in achieving better stability of the individual plants. Further studies are necessary, also to include the biomechanic aspect (NIKLAS 1992). Moreover, even in turnip plants, such as *Foeniculum vulgare*, stability is an important factor, especially when remembering that the leaf rosette is located several centimeters above the soil surface at the beginning of development. Good stability is achieved by downward movement of the rosette, caused by contraction of the turnip (TROLL 1937–1943; STEIN & WEBERLING 1992). In conclusion, from a functional point of view, plant stability functions alongside anchorage systems, previously examined for annual dicots several times (e.g., ENNOS & FITTER 1992; ENNOS et al. 1993). However, observations about the seedlings and the possible role of root or stem contraction have not been taken into account to date.

References

BRUCH, H., 1953, Beiträge zur Morphologie und Entwicklungsgeschichte der Fenchelwurzel (*Foeniculum vulgare* MILL.). Beitr. Biol. Pflanzen, **32**, 1–26.
BUSSEN, M., 1951, Untersuchungen über die Bewurzelung der Keimpflanzen im Verwandtschaftskreis der Monokotylen. Dissertation, Mainz, published as manuscript.
ENNOS, A. R.; FITTER, A. H., 1992, Comparative functional morphology of the anchorage systems of annual dicots. Func. Ecol., **6**, 71–78.
ENNOS, A. R.; CROOK, M. J.; GRIMSHAW, C., 1993, A comparative study of the anchorage systems of himalayan balsam *Impatiens glandulifera* and mature sunflower *Helianthus annuus*. J. Exp. Bot., **44**, 133–146.

FROEBE, H. A.; PÜTZ, N., 1988, Orientierende Versuche zur Verlagerung pflanzlicher Organe im Erdboden durch definierte Kräfte. Beitr. Biol. Pflanzen, **63**, 81–100.

GALIL, J., 1983, Morpho-ecological studies of lowering in the seedling of the geophyte *Ixiolirion tataricum* (PALL.) HERB. New Phytol., **143**, 143–150.

JERNSTEDT, J., 1984, Seedling growth and root contraction in the soap plant, *Chlorogalum pomeridianum* (Liliaceae). Amer. J. Bot., **71**, 69–75.

NIKLAS, K. J., 1992, Plant biomechanics. An engineering approach to plant form and function. Chicago.

NORDHAUSEN, M., 1913, Über kontraktile Luftwurzeln. Flora, **105**, 102–126.

PÜTZ, N., 1993, Underground plant movement. I. The bulb of *Nothoscordum inodorum* (Alliaceae). Botanica Acta, **106**, 338–343.

PÜTZ, N., 1996 (in press), Underground plant movement. III. The corm of *Sauromatum guttatum* (Araceae). Flora, **191**.

PÜTZ, N.; HÜNING, G.; FROEBE, H. A., 1995, Cost and advantage of soil channel formation by contractile roots in successful plant movement. Ann. Bot., **75**, 633–639.

RIMBACH, A., 1897a, Lebensverhältnisse des *Allium ursinum*. Ber. Deutsch. Bot. Ges., **15**, 248–252.

RIMBACH, A., 1897b, Biologische Beobachtungen an *Colchicum autumnale*. Ber. Deutsch. Bot. Ges., **15**, 298–302.

RIMBACH, A., 1921, Über die Verkürzung des Hypocotyls. Ber. Deutsch. Bot. Ges., **39**, 285–287.

RIMBACH, A., 1928, Wachstumsweise der Calla *(Zantedeschia aethiopica)*. Angew. Bot., **10**, 148–152.

STEIN, U.; WEBERLING, F., 1992, Wuchsformuntersuchungen im Páramo Costa Ricas. I. Einführung. II. *Acaena cylindristachya* RUIZ ET PAVON, *Acaena elongata* L. (Rosaceae-Sanguisorbae) und *Chusquea subtesselata* HITCHCOCK (Poaceae). Flora, **187**, 369–402.

TILLICH, H. J., 1992, Bauprinzipien und Evolutionslinien bei monocotylen Keimpflanzen. Bot. Jahrb. Syst., **114**, 91–132.

TROLL, W., 1937–1943, Vergleichende Morphologie der höheren Pflanzen. Erster Band: Vegetationsorgane. Berlin.

VRIES, H., DE, 1880, Ueber die Kontraktion der Wurzeln. Landwirthschaftl. Jahrb., **9**, 37–95. In HUGO DE VRIES, Opera e Periodicis collata. Vol. II, Utrecht, A. Osthoek.

WOODHEAD, T. W., 1904, Notes on the bluebell. The Naturalist, **566**, 41–48, 81–88.

ZIMMERMANN, M. H.; WARDROP, A. B.; TOMLINSON, P. B., 1968, Tension wood in aerial roots of *Ficus benjamina* L. Wood. Sci. Technol., **2**, 95–104.

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