

Seedling establishment, bud movement, and subterranean diversity of geophilous systems in Apiaceae

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Summary

Geophilous systems of plants are not only regarded as organs of underground storage. Such systems also undergo a large range of modifications in order to fulfill other 'cryptical' functions, e.g. positioning of innovation buds, vegetative cloning, and vegetative dispersal. Seedlings should always be the point of departure for any investigation into the structure of geophilous systems. This is because in the ability to survive of geophilous plants it is of primary importance that innovation buds can reach a safe position in the soil by the time the first period hostile to vegetation commences.

Our analysis of such systems thus focused on examining the development of 34 species of the Apiaceae, beginning with their germination. Independent of life-form and life-span, all species exhibit noticeable terminal bud movement with the aid of contractile organs. Movement was found to be at least 5 mm, reaching a maximum of 45 mm. All species exhibit a noticeable contraction of the primary root. In most cases the contraction phenomenon also occurs in the hypocotyl, and some species show contraction of their lateral and / or adventitious roots. Analysis of movement shows the functional importance of pulling the innovation buds down into the soil. Furthermore, in many species it becomes obvious that, even in the first year of development, modifications of the geophilous system take place in order to fulfill other cryptical functions.

Finally, our functional viewpoint highlights the redundancy of differentiating between Raunkiaer's cryptophytes and hemicryptophytes, and proposes that plants surviving at least one unfavorable season in the soil should all be subsumed in one category, the geophilous plants.

Key words: Apiaceae, root contraction, seedling, plant movement, geophytes, establishment, life forms.

Introduction

After germination, the further adaptational development of Central European plants is geared towards surviving the first unfavorable season. Therefore, RAUNKIAER (1934) characterized distinct life-forms, later expanded into life strategies (GRIME 1988; FREY 2000). However, FREY & LÖSCH (1998) made clear that examination of how seedlings establish themselves in terms of these survival strategies is very far from complete.

Furthermore, when approaching from the dualism of 'form and function' (PÜTZ & SCHMIDT 1999), analysis of the autecology of species must start with seedling development. Accordingly, for example, it is essential for geophytes to get even first year innovation buds into a safe underground position. Within the Apiaceae, PÜTZ

& SUKKAU (1995) demonstrated this bud positioning during the development of *Foeniculum* seedlings by the phenomenon of contraction. At the same time, developmental studies of *Anthriscus sylvestris* and *Aegopodium podagraria* (SUKKAU & PÜTZ 2001) proved that the geophilous basis of life strategy is established in the first year of development.

Further autecological analysis of seedling establishment in Apiaceae has not yet been completed. This raises the question as to whether or not the movement of innovation buds by contraction is a general phenomenon in Apiaceae geophytes. At the same time, in Apiaceae other life-forms exist, and it can be expected that (for example) in therophytes or phanerophytes, bud positioning in the soil is not necessary, thus making moving activity unlikely.

Overall it can be said that information about the geophilous systems in Apiaceae is still very incomplete. So, beginning with germination, the development of a large number of species has been analyzed in this study. The aim is to achieve a basic knowledge of subterranean diversity of geophilous systems in Apiaceae.

Material and methods

Germination and seedling establishment of the following 34 species were examined: (place of origin of the diaspores: BG Ac – Botanical Garden, Aachen, Germany; Se We – Weiser seed store, Aachen; Se Je – Jelitto seed store, Schwarmstedt; OP – original place, PC Sch – private collection of K. Schmidt, Krefeld, Germany).

Aegopodium podagraria L. (OP Aachen-Dorbach); *Ammi visnaga* L. (BG Ac); *Anethum graveolens* L. (Se We); *Angelica sylvestris* L. (BG Ac); *Anthriscus cerefolium* HOFFM. (Se We); *Anthriscus sylvestris* HOFFM. (OP Kall, Eifel, Germany); *Apium graveolens* var. *dulce* MILL (Se We); *Astydamia latifolia* BAILLON (PC Sch); *Chaerophyllum bulbosum* L. (PC Sch); *Chaerophyllum temulum* L. (PC Sch); *Cicuta virosa* L. (BG Ac); *Crithmum maritimum* L. (PC Sch); *Cryptotaenia elegans* WEBB EX BOLLE (PC Sch); *Eryngium maritimum* L. (Se Je); *Eryngium planum* L. (PC Sch); *Ferula latipinna* SANTOS (PC Sch); *Ferula communis* L. (Se Je); *Heracleum sphondylium* L. (OP Aachen, Steppenber); *Laserpitium siler* L. (BG Ac); *Levisticum officinale* KOCH (Se Je); *Melanoselinum decipiens* HOFFM. (PC Sch); *Meum athamanticum* JACQ. (Se Je); *Oenanthe javanica* DC. (OP Aachen, Broichbach); *Oenanthe silaifolia* M. BIEB. (BG Ac); *Orlaya grandiflora* HOFFM. (PC Sch); *Pastinaca sativa* L. (Se We); *Petroselinum crispum* ssp. *tuberosum* SOO (Se We); *Peucedanum altissimum* THELL (Se Je); *Peucedanum officinale* L. (BG Ac); *Peucedanum ostruthium* KOCH (Se Je); *Pimpinella anisum* L. (Se Je); *Scaligeria cretica* BOISS. (PC Sch); *Smyrniolum olus-atrum* L. (BG Ac); *Tordylium maximum* L. (PC Sch).

The diaspores were seeded (1) directly and (2) after stratification. For stratification, diaspores were placed in Petri dishes (diameter 13 cm) on wet filter paper. The covered Petri dishes were stored at 4 °C for 4 weeks (HEROLD 1958).

Diaspores of all species were grown in the greenhouse of the Botanical Garden of the RWTH Aachen. We used specific photo-containers (see PÜTZ 1993, 1998; PÜTZ & SUKKAU 1995), as well as commercial plant pots (Teku Container, 20 cm, Asperg, Köln, Germany).

Germination temperature was a minimum of 12 °C, and after germination plants were grown at a minimum temperature of 14 °C. On hot summer days, the temperature was increased to 35 °C, but was normally approx. 20–22 °C. In addition to sunlight exposure, plants were illuminated for 12 h daily (Osram lamps – Power-Star HQI-T 400 W/DH).

The standard soil was a mixture (1:1:1) of sand, loam and TKS 1 (Asperg, Köln, Germany). 10 weeks after germination seedlings were fertilized with Wuxal-Super (Aglukon, Düsseldorf, Germany) at a concentration of 0.2% at 5 week-intervals.

When sowing, a control mark (white plastic marker, 15 mm long, 2 mm in diameter) was placed two centimeters from the diaspores. The vertical distance from the control mark to the growing cryptocorm showed the underground movement. Thus, soil movement, e.g. subsidence, was prevented from distorting our measurements. Three diaspores were placed in each container and covered with dry riddled sand until the diaspore position was 10 mm below the soil surface. During germination, the containers were covered by transparent covers.

The movement of a minimum of three individuals of each species was examined carefully by digging them out at regular intervals (every 1–4 weeks). Digging is from one side only, and after examination, the container was very carefully refilled with substratum (see PÜTZ 1993). Time lapse photographs (see PÜTZ 1993, 1996, 2002) were made from several species. Photos were taken with an Olympus OM-2, aperture 16 (Agfa pan APX 25) mounted on a tripod (GIZO, Gilux reporter) to ensure that the distance from the plant was the same in each photo.

Individual curves of movement were obtained by measuring the movement of the first innovation buds (cotyledonous buds) versus the time of examination (number of weeks after germination).

Results

Time lapse photography is the best way of demonstrating underground seedling development. Examples of these photo series are presented here for three species (Fig. 1), which represent typical life-forms in Apiaceae. The annual *Anthriscus cerefolium* elongates its hypocotyl to a length of approx. 20 mm (in the case study of Fig. 1 the length is 24 mm), and cotyledons and the apical cone are thus 14 mm above the soil surface at the end of the second week. During the next seven days, the hypocotyl contracts by 11 mm. This is followed by a measurable, continuous shortening of the primary root, and thus an overall shortening of 24 mm is visible after 9 weeks (see movement curve in Fig. 2A). 25 weeks after germination the plant begins flowering, and dies without any further contraction of root after a life-span of approx. 6 months.

Astydamia latifolia, a biennial to pluriennial species, elongates its hypocotyl, and the apical cone becomes positioned approximately 2 mm above the soil surface. At the base the cotyledons grow together to form a tube, which encloses the shoot tip over a length of approx. 2 mm. After 7 weeks, a small turnip has been formed, although, even at this time, its contraction ability has moved the basis leaf rosette into the soil. The single photos in Fig. 1 B show a continuous downward movement of the shoot base, which, after 23 weeks, can be found 30 mm below the soil surface (see Figure 2B).

The tree-shaped *Cryptotaenia elegans* elongates the hypocotyl and establishes the cotyledons approx. 3 mm above the soil surface (Figure 1C). Up to the 12th week

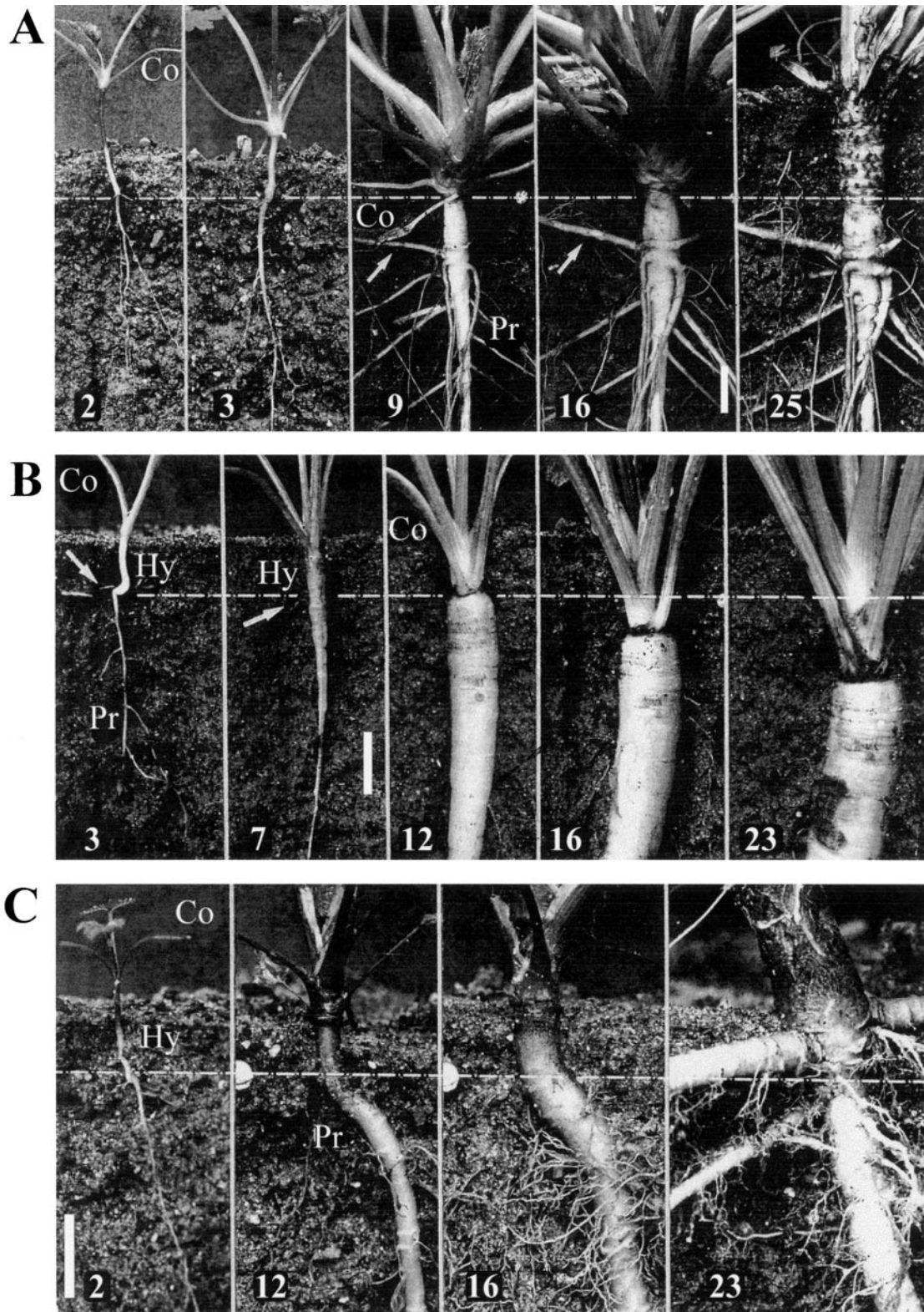


Fig. 1. Time-lapse photography of (A) *Anthriscus cerefolium*, (B) *Astydamia latifolia*, (C) *Cryptotaenia elegans*. The number in the lower section of each photo gives the time of examination after germination in weeks. The white line is the control mark. The bar represents 10 mm. **Co** – cotyledon, **Hy** – hypocotyl, **Pr** – primary root. The arrow points to the secondary repositioning of a lateral root.

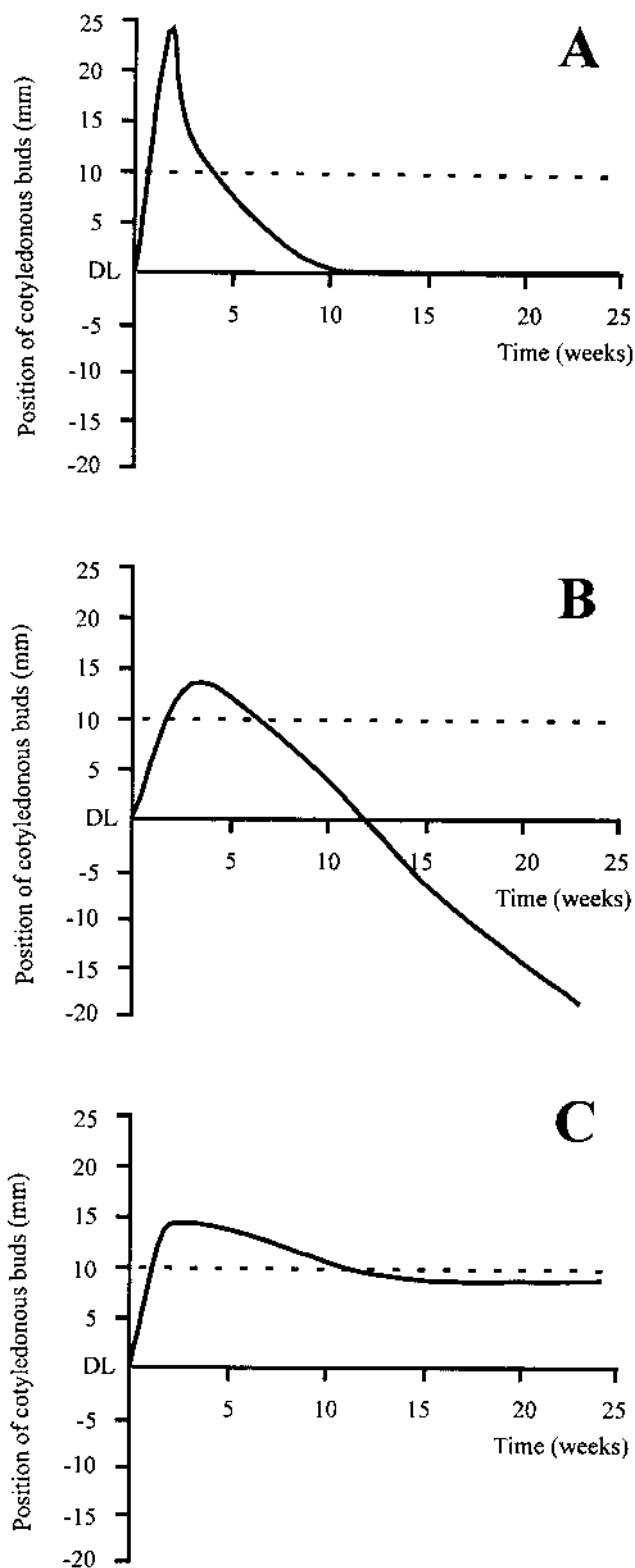


Fig. 2. Movement curves of (A) *Anthriscus cerefolium*, (B) *Astydamia latifolia*, (C) *Cryptotaenia elegans*. The dotted line represents the soil surface. DL refers to the diaspore level at the beginning of measurement (= 10 mm below the soil surface).

of development, a contraction of the primary root occurs, pulling the base of the cotyledons 4 mm down (see Figure 2C). After this, no further downward movement is visible [After several vegetative years *Cryptotaenia elegans* develops axillar inflorescences. After fructification, the tree-shaped plants die (HOHENESTER & WELB1993). *Cryptotaenia elegans* is one of few Apiaceae with a life-form which can be described as “hapa-xanth phanaerophyte”].

Not only the examples presented here, but all species we examined exhibit the contraction phenomenon, although to varying degrees (Table 1). In all species the primary root shortens actively, as does, in most cases, the hypocotyl. In several species this active shortening of the hypocotyl reaches more than 60% (e.g., *Angelica sylvestris*, see table 1). Furthermore, a few species show lateral root contraction (e.g., *Laserpitium siler*, *Eryngium maritimum*) or adventitious root contraction (e.g., *Cicuta virosa*, *Oenanthe javanica*). The degree of contraction varies from species to species (Table 1). In most cases, contraction was higher than a span of 15 mm (with a maximum of 45 mm in *Peucedanum altissimum*). Only 7 species show a contraction which is lower (less than 10 mm), with a minimum of 3 mm (*Ferula latipinna*, *Smyrniolum olus-atrum*).

In contrast to this downward movement, there was an earlier elongation of the hypocotyl. In a few species, hypocotyl elongation was very slight or completely absent (*Scaligeria cretica*, *Chaerophyllum bulbosum*). However, in most cases it was approx. 10–15 mm. Only in a few cases this elongation was much greater (*Anthriscus cerefolium*, 18–24 mm; *Anethum graveolens*, 25–35 mm).

Taking the cotyledonous buds as a benchmark for comparison, the oppositely directed movements result in a specific position relative to soil surface at the end of the first vegetation period (Table 1). On one hand, a small group of species becomes apparent, those reaching a bud position closer to the soil surface than the starting diaspore level of 10 mm. These species belong to the therophytes (e.g., *Anethum graveolens*, *Pimpinella anisum*) or the phanerophytes (e.g., *Cryptotaenia elegans*, *Melanoselinum decipiens*). A second group of species show balanced movement (e.g., *Ferula latipinna*, *Anthriscus cerefolium*), and their bud position at the end of the (first) vegetation period is at a level of 10–15 mm, very close to the previous diaspore level (10 mm). However, most species showed strong downward movement, and their cotyledonous buds were laying – when starting at a diaspore level of 10 mm – at a depth of 20–45 mm (e.g., *Meum athamanticum*, *Anthriscus sylvestris*).

Time correlation in reaching this position can be shown in the movement curves, and our measurements revealed different types of movement. Many thermo-

Table 1. Measurement of movement of Apiaceae geophilous systems (in mm, average of 3 single measurements). Elo-hy – elongation of the hypocotyl, loc-con – site of contraction, Con-mo – contraction movement, To-Mov - total movement after 24 weeks, + : upwards movement, - : downward movement of the cotyledonous buds. In 'to-mov' the entries define the position of the buds in relation to the diaspore level. Pr – primary root; hy – hypocotyl, aR – adventitious roots, IR – lateral roots.

	Species	Elo-hy	loc-con		Con-mo	To-mov	
1	<i>Aegopodium podagraria</i>	+15	Pr	hy	aR	20	-5
2	<i>Amni visnaga</i>	+10	Pr			10	-0
3	<i>Anethum graveolens</i>	+29	Pr	hy		5	+24
4	<i>Angelica sylvestris</i>	+10	Pr	hy (66%)		25	-15
5	<i>Anthriscus cerefolium</i>	+20	Pr	hy (62%)		22	-2
6	<i>Anthriscus sylvestris</i>	+11	Pr	hy (65%)		35	-24
7	<i>Apium graveolens</i>	+19	Pr	hy		25	-6
8	<i>Astydamia latifolia</i>	+12	Pr	hy		32	-20
9	<i>Chaerophyllum bulbosum</i>	-4	Pr			11	-15
10	<i>Chaerophyllum temulum</i>	+13	Pr	hy (55%)		28	-15
11	<i>Cicuta virosa</i>	+10	Pr		aR	24	-14
12	<i>Crithmum maritimum</i>	+10	Pr			20	-10
13	<i>Cryptotaenia elegans</i>	+13	Pr			4	+9
14	<i>Eryngium maritimum</i>	+20	Pr	hy	IR	25	-5
15	<i>Eryngium planum</i>	+10	Pr	hy		30	-20
16	<i>Ferula latipinna</i>	+2	Pr			3	-1
17	<i>Ferula communis</i>	+11	Pr	hy		30	-19
18	<i>Heracleum sphondylium</i>	+10	Pr	hy		13	-3
19	<i>Laserpitium siler</i>	+7	Pr	hy	IR	18	-11
20	<i>Levisticum officinale</i>	+15	Pr	hy (60%)		30	-15
21	<i>Melanoselinum decipiens</i>	+13	Pr	hy		5	+8
22	<i>Meum athamanticum</i>	+8	Pr	hy		40	-32
23	<i>Oenanthe javanica</i>	+10	Pr	hy	aR	20	-10
24	<i>Oenanthe silaifolia</i>	+10	Pr	hy	IR	24	-14
25	<i>Orlaya grandiflora</i>	+10	Pr	hy		15	-5
26	<i>Pastinaca sativa</i>	+15	Pr	hy		25	-10
27	<i>Petroselinum crispum</i>	+20	Pr	hy (60%)		30	-10
28	<i>Peucedanum altissimum</i>	+10	Pr	hy		45	-35
29	<i>Peucedanum officinale</i>	+10	Pr	hy		22	-12
30	<i>Peucedanum ostruthium</i>	+10	Pr	hy		40	-30
31	<i>Pimpinella anisum</i>	+9	Pr	hy		5	+4
32	<i>Scaligeria cretica</i>	-2	Pr			9	-11
33	<i>Smyrniolum olus-atrum</i>	+3	Pr			3	0
34	<i>Tordylium maximum</i>	+14	Pr	hy	IR	15	-1

phytes (Fig. 3 A) exhibit a rapid up and down movement of their cotyledonous buds, completed 10–15 weeks after germination. However, some therophytes (e.g., *Anethum graveolens*, *Pimpinella anisum*) and the phanerophytes (*Cryptotaenia elegans*, *Melanoselinum decipiens*), show only limited downward movement (compare Fig. 2C).

The movement of biennial or perennial turnips is very similar, although downward movement is more pronounced, lasting at least 20 weeks and reaching a greater depth (Fig. 3B, turnip movement).

A few species make very unusual movements. Thus, in *Scaligeria cretica* and *Chaerophyllum bulbosum* (Fig. 3C) there is a total lack of hypocotyl elongation, compensated for by an obvious doubled downward

movement. At the same time, *Smyrniolum olus-atrum* and *Ferula latipinna* show only very slight total movement.

These characteristic movements are correlated with a characteristic seedling morphology. The most frequent seedling type is the T-type (Fig. 4), which shows hypocotyl elongation, thus pushing the cotyledonous buds upwards. Subsequent contraction has to compensate for this primary upward movement (see Fig. 3A, B). In seedlings of the V-type (Fig. 4), hypocotyl elongation remains very slight, and therefore only a small contraction suffices for maintaining the diaspore level (moving type of *Smyrniolum olus-atrum* and *Ferula latipinna*). Finally, the moving type in Fig. 3C is produced by the Y-type of seedlings (Fig. 4). A cotyledonous tube is formed, pushing the innovation buds some millimeters

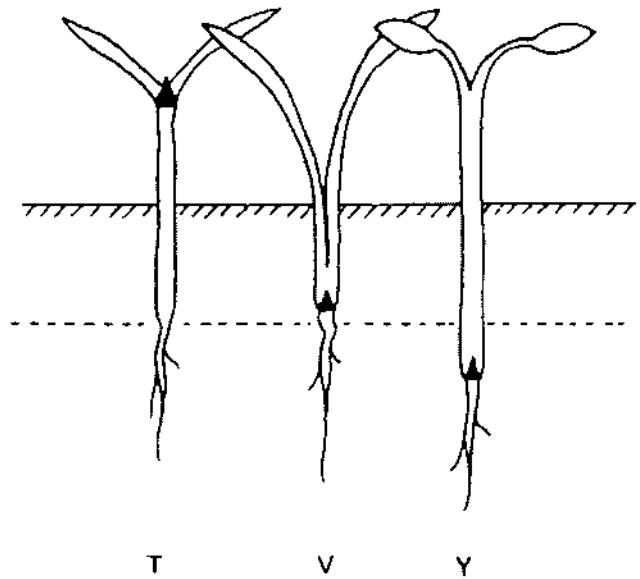
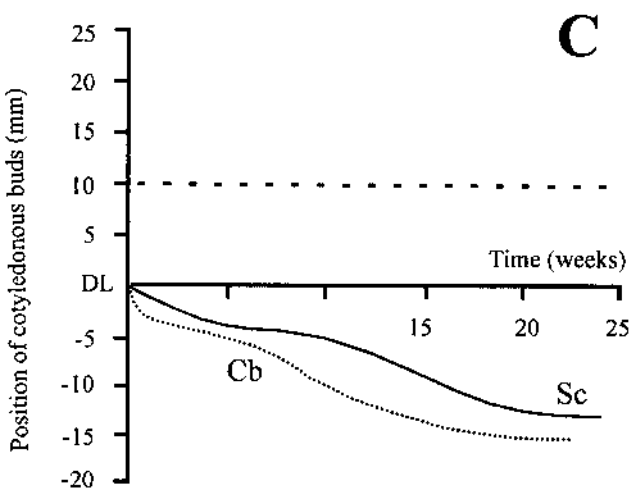
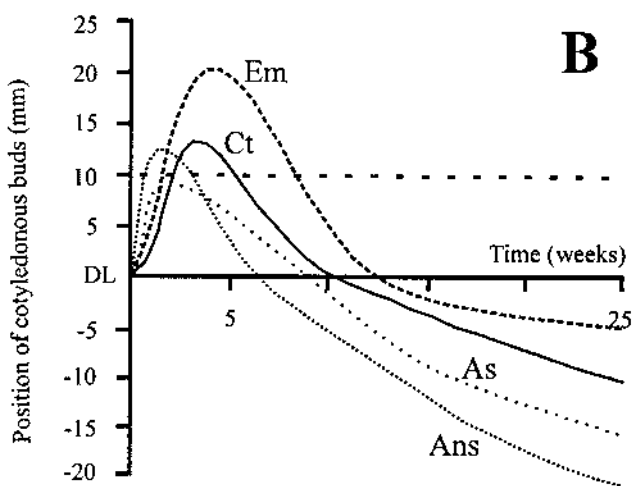
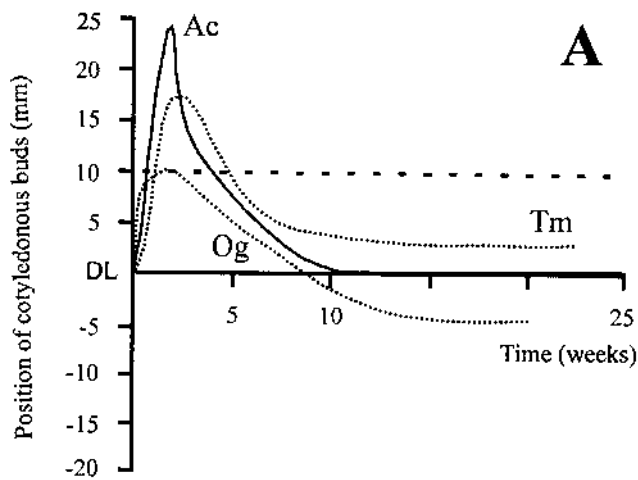


Fig. 4. Three different types of seedlings in Apiaceae. The black triangles show the position of the apical cone. The dotted line shows the level of seeding and the soil surface is hatched.

down into the soil. Subsequently, only slight contraction of the primary root is necessary to reach a safe soil depth (Fig. 3C).

Discussion

As our results show, contraction is an almost general feature in Apiaceae. Turnip contraction, pronounced in some species, has been known about for many years (e.g., DE VRIES 1880; RIMBACH 1898, 1929; TROLL 1937). However, the generalization is still very surprising. Unfortunately, due to a lack of germinable diaspores, examination of a few interesting species has not been successful up to the present. For example, it is not known how the cryptocorm of *Bunium bulbocastanum*, which is described as a perennial hypocotyl corm (after TROLL 1937), reaches a soil depth of 20 cm (HEGI 1931). Furthermore, analysis of the development in rhizomatous plants (e.g. *Sanicula europaea*) is still lacking.

Fig. 3. Typical underground movements in the family of the Apiaceae. (A) Movement of therophytes (Og – *Orlaya gigantea*, Tm – *Tordylium maximum*, Ac – *Anthriscus cerefolium*). (B) Movement of perennial herbs (As – *Angelica sylvestris*, Ans – *Anthriscus sylvestris*, Ct – *Chaerophyllum temulum*, Em – *Eryngium maximum*). (C) Movement of Y-type plants (Cb – *Chaerophyllum bulbosum*, Sc – *Scaligeria cretica*). The dotted line represents the soil surface and DL the diaspore level at the beginning of measurement (= 10 mm below the soil surface).

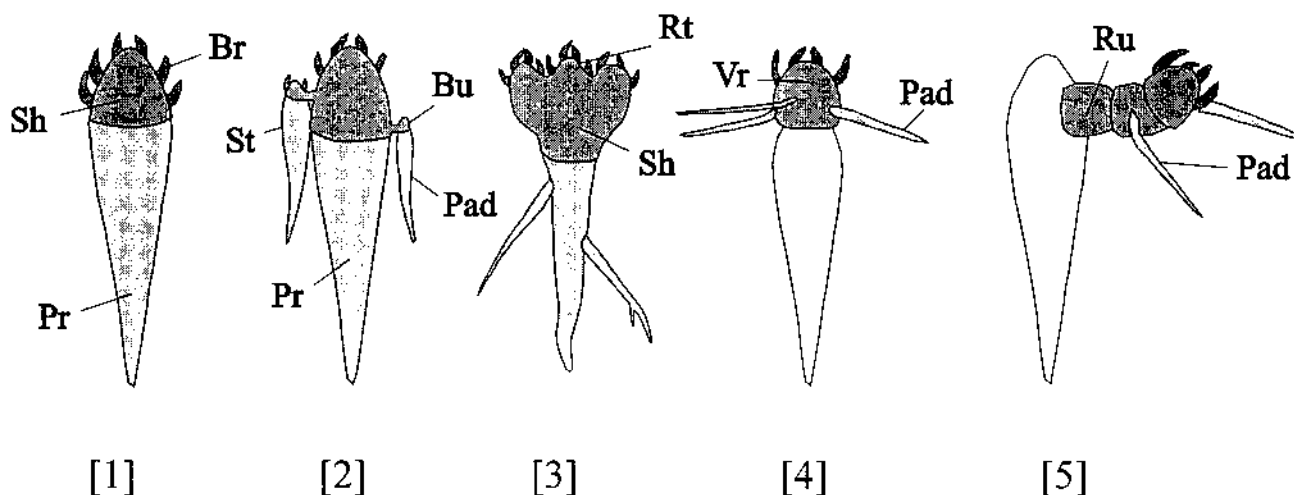


Fig. 5. Schematic diagram of the diversity of geophilous systems within the Apiaceae: [1] turnip, [2] secondary turnip, [3] pleiocorm, [4] vertical rhizome, [5] runner. **Br** – bract, **Bu** – buds, **Pad** – adventitious roots, **Pr** – primary root, **Rt** – rhizomatous head of the turnip, **Ru** – runners, **Sh** – shoot (part of the turnip), **St** – secondary turnip, **Vr** – vertical rhizome.

The explanation of the anatomical mechanism responsible for the ability to contract the geophilous parts of the plants presents some difficulties. Earlier anatomical examinations in Apiaceae investigated only one stage of root development, and were thus unable to detect the contraction phenomenon (BRUCH 1953; LIERMANN 1926; ESAU 1940; ESCHRICH 1963; KUTSCHERA & SOBOTIK 1992). The most useful early approach to the anatomical mechanism of contraction in Apiaceae was the study by BERCKEMEYER (1928), who discovered growing cell nests bending longitudinal tissue elements (e.g. resin ducts). BERCKEMEYER supposed that this bending created a longitudinal tension responsible for the contraction of the turnip. At the same time, it seems useful to investigate the possibility of realization of the “pneu model” (PÜTZ 1999) in Apiaceae.

A general contraction during germination and the first life-span signifies also general movement. However, movement of the innovation buds cannot be the only function. In therophytes at least this reason for the phenomenon appears illogical. It can be assumed that root contraction may function in steadying the plant (KIRSCHNER et al. 1934), and we must hope that biomechanical approaches will provide us with further information in this respect. It seems interesting to note that already SACHS (1873: 419) observed root contraction at the growing zone of roots and discussed its role in the context of the biomechanics of root growth.

However, especially in plants with geophilous systems, the primary function of root and stem contraction is obvious, because it results in a downward movement of the innovation buds approaching by this way safe sites for them. Within the Apiaceae there is a great diversity achieving this goal:

[1] In many species the turnip itself contracts, as it is familiar from many turnips of species of other families (e.g., *Mirabilis jalapa*, Nyctaginaceae, GLUTH & PÜTZ 2001; *Trifolium pratense*, Fabaceae, DE VRIES 1880; *Bryonia alba*, Cucurbitaceae, TROLL 1937: 166).

[2] In *Anthriscus sylvestris*, this ability is transmitted to adventitious roots, which develop into secondary turnips (SUKKAU & PÜTZ 2001).

[3] Perennial plants of longer life-span often form pleiocorms [“Rüben mit rhizomartigem Rübenkopf” (“turnips with a rhizomatous turnip head). cf. MEUSEL 1951]. A good example for pleiocorms in Apiaceae is *Levisticum officinale* (unpublished).

[4] The cryptocorms of several species become modified into vertical rhizomes (e.g., *Cicuta virosa*, TROLL 1937). In the first phase, the plants show contraction of the primary root, but then they have a further rhizome movement, caused by the contraction activity of the adventitious roots. This movement (unpublished observations) is very similar to that of typical monocotyledons (e.g., *Hypoxis setosa*, ARBER 1925, *Hemerocallis fulva*, PÜTZ 1998).

[5] Finally, *Aegopodium podagraria* exhibits a cryptocorm-metamorphosis (SUKKAU & PÜTZ 2001). In the first year, development of this species starts with the formation of a turnip. However, after several weeks runners for vegetative dispersal appear. Small vertical rhizomes grow at the tips of these runners and become pulled down by the strong contraction activity of the adventitious roots.

It seems appropriate to present the morphological structuring within the diversity of geophilous systems schematically (Fig. 5). The basic cryptocorm system in Apia-

ceae is formed by the primary root, which in the case of many geophytes develops into a turnip ([1] in Fig. 5). At the same time, perennial plants, especially of longer life-span, show typical modifications, and in some cases even cryptocorm metamorphosis becomes evident: The formation of vertical rhizomes ([4] in Fig. 5) might be an adaptation to wet habitats (WEHSARG 1935), while the formation of ramets (vegetative cloning) is useful in occupying a useful habitat ([2] and [4] in Fig. 5). Creating runners enables vegetative dispersal, which is, in the case of *Aegopodium podagraria*, very successful ([5] in Fig. 5). All these principles of the geophilous survival strategy can be analyzed during the development of seedlings. Therefore, the first year of development is not only important in positioning the innovation buds, but provides the basis for subsequent cloning and also for dispersal patterns.

The diversity of geophilous systems results in a number of different underground complexes, which are not only interesting in a morphological context, but have different autecological functions (PÜTZ & SCHMIDT, 1999). However, our examinations of the family of the Apiaceae make clear that a simple “functional” division into hemicryptophytes and cryptophytes (RAUNKIAER 1934) is, in many cases, too vague. Already at the end of the first vegetation period, the innovation buds of all biennial or perennial herbs examined here are unequivocally below the soil surface. They are all “geophytes” (according to RAUNKIAER’s definition). From a functional point of view it seems completely unnecessary to differentiate between hemicryptophytes and cryptophytes: they all are just ‘geophytes’ or ‘geophilous plants’: plants possessing geophilous organ systems to survive at least one unfavorable season (dry summer, cold winter) in the soil. By this definition, more than half of the Central European species are geophilous plants. Such a big group has to be sub-divided, and the life strategies of FREY & HENSEN (1995; cf. FREY 2000) might point in the right direction. However, careful examination of the ecological functionality of the geophilous systems will first have to be completed.

Modes of existence are imprinted in the first year (SUKKAU & PÜTZ 2001), and FREY & LÖSCH (1998) underlined the necessity of examining how seedlings establish themselves. Within the Apiaceae, several types of seedlings of different functional adaptation were found. In addition to the normal T-type, a few species possessing other seedling types were found (Y or V, Fig. 4, cf. HACCIUS 1952). These types also prefer other movement strategies: (1) active ones by downward pushing of the innovation zone (similar cases in other families: RIMBACH (1897) for *Allium ursinum*; GALIL (1983) for *Ixiolirion tataricum*; PÜTZ & SUKKAU (1995) for *Pancratium maritimum*; GLUTH & PÜTZ (2001) for *Mirabilis jalapa*); or (2) only passive ones

with an absence of hypocotyl elongation. HACCIUS (1952) explained the V- and Y-types as an evolutionary adaptation to scarce and irregular rainfall. In fact, the species examined here settle in disturbed areas with quickly drying soil surfaces. It is clear that experimental ecological approaches are necessary to establish a clear correlation between the morphological structures and the habitat conditions. Moreover, the general feature of root and stem contraction in Apiaceae needs further examination in terms of anatomical, morphological, physiological, ecological, and evolutionary factors, or, to put it simply, in terms of plant construction modes according to SCHMIDT & PÜTZ (1999).

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