

Seedling establishment, underground kinetics, and clonal reiteration: How do *Potentilla inclinata* and *Inula ensifolia* get their multifunctional subterranean systems?

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Abstract

The development of a seedling into an adult plant comprises various underground processes. Time-lapse photography (TLP) makes them visible. This is documented for *Potentilla inclinata* (Rosaceae) and *Inula ensifolia* (Asteraceae).

After germination, *P. inclinata* develops a taproot system. Contraction phenomena pull the basal part of the shoot at least 10 mm into the soil. Later, several adventitious roots are generated, and thus the root system changes to a fibrous one. This is followed by cloning without separation of the ramets.

Seedlings of *I. ensifolia* develop a weak primary root. At an early stage, adventitious roots are formed at the leaf rosette. This fibrous root system exerts a strong pulling effect on the shoot. After one vegetation period the basis of the rosette is approx. 30 mm under the soil surface. Cloning includes the formation of many new horizontal shoots, which conquer new sites.

These two examples show three functional steps common in the developmental progress of subterranean systems: (I) establishment of the seedling, (II) innovation and survival of the young plant, and (III) reiteration (cloning and dispersal). However, to accomplish these basic development steps the diversity of subterranean systems is enhanced by different organographical components.

Furthermore, the development of subterranean systems is a dynamic process consisting of two kinetic processes: the vertical movement during seedling establishment, which brings the innovation buds to a safe soil position, and the horizontal movement during dispersal, which conquers new sites.

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Introduction

Rhizomes, bulbs, or turnips are statically fixed in the soil, their main function being nutrient storage. State-

ments like this, which can be found in many botanical textbooks, do not take into account some further important aspects for the plant, such as survival, holding a site occupied, clonal growth, and vegetative dispersal (see e.g. Brock et al., 2000; Stöcklin, 1992; Troll, 1937; Winkler and Stöcklin, 2002).

Furthermore, underground organs are not statically fixed in the soil, but move, for example, to bring

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innovation buds into a favourable position for surviving cold winters or hot summers (see Galil, 1980, 1981; Pütz, 2002; Rimbach, 1898). Growth of the plant results from some of these movements, while in many other cases, contraction processes allow plants to move. External stimuli induce these movements (Galil, 1958; Halevy, 1986; Pütz, 1996, 1998; Pütz et al., 1997). In many cases, the whole organism participates in the movement, as observed in *Lapeirousia laxa* (Pütz and Sukkau, 1995) or *Arum maculatum* (Rimbach, 1897). Generally, movements are relatively short and slow (e.g. seedlings of *Chlorogalum pomeridianum* move 63.8 ± 19.4 mm in a period of 29 weeks, Jernstedt, 1984).

The observation of a dug-out plant cannot reveal its mobility potential. Time-lapse photography (TLP) is an appropriate method for this purpose (Pütz, 1993, 1998; Pütz and Sukkau, 2002). TLP enables us to follow the underground development of a plant, from seedling establishment to the complex underground system (e.g., Pütz, 1996; Pütz and Sukkau, 1995; Sukkau and Pütz, 2001).

Subterranean systems exhibit high variation, accomplish many different functions, and are also mobile. Observations of the underground growth of non-woody perennials would reveal many ecological adaptations. In fact, these observations are made possible by increasing the time of examination in time lapse photography. These series render it visible how different functions and mobile phases interact in the overall progress of subterranean systems. In addition to providing two examples of this kind of development of multifunctional underground systems, this paper also presents a broader discussion of typical steps commonly encountered in the developmental progress of subterranean systems.

Materials and methods

We received diaspores of *Inula ensifolia* L. (Asteraceae) from the Botanical Garden of the University of Vienna (Austria). Diaspores of *Potentilla inclinata* Villars (Rosaceae) were collected in Gönnersbohl near Hitzingen, Konstanz County, Baden-Wuerttemberg, Germany.

Diaspores were seeded in commercial plant pots (Pöppelmann container TC 201 Schwarz, volume 10l) prepared as specific photo-containers (cf. Pütz, 1993, 1998; Pütz and Sukkau, 2002). These containers enable us to dig out the plants from one side. The standard soil was a mixture (1:1) of sand, and garden mould (profisubstrat, gramoflor, Vechta). From 12 weeks after germination, seedlings were fertilised with Wuxal-Super 8-8-6 (N-P-K; Aglukon, Düsseldorf, concentration 0.5%) at three weekly intervals.

At sowing, a control mark (plastic peg, 15 mm long, 4 mm in diameter) was placed 2 cm from the diaspore. The vertical distance from the control mark to the growing system was the marker for underground

movement. In this way, soil movement, especially subsidence, could not distort our observations. Five diaspores were placed in each container and covered with dry riddled soil until the diaspore position was 10 mm below the soil surface.

For each species, five pots with at least two individuals were cultivated in a culture room at a minimum temperature of 14 °C and a maximum temperature of 28 °C. Plants were illuminated for 12 h daily (Philips Powertone Sow-T plus 400 W). For at least 12 months, the underground movements of the plants were carefully examined at regular intervals (every 1–4 weeks). For examination one-half of the pot was removed. After examination, the restored container was carefully refilled with substratum (see Pütz, 1993). Photographs were made with a digital camera (Casio QV 400). On PC (Intel P4, 3 GHz, Corel Draw 11.0), pictures of each plant were joined to TLP (see Pütz, 1993, 1996, 2002).

Furthermore, three pots of each species were cultivated outdoors, exposing them to the (rather mild) winter conditions of Northwest Germany.

Results

The mere descriptions of the underground plant parts of *I. ensifolia* and *P. inclinata* are incomplete and unsatisfactory. In general both taxa are regarded as hemicryptophytes (Gerstberger, 2003; Wagenitz, 1979). For instance, the underground system of *P. inclinata* (Fig. 1A) is described by Gerstberger (2003, p. 150) as “Ausdauernde ... Rosettenstaude, Wurzelstock mit Pfahlwurzel, ein- bis mehrköpfig.” [perennial ... rosette plant, root stock with a tap root, one to multi-shooted]. Wagenitz (1979, p. 176) describes the underground system of *I. ensifolia* (see Fig. 1B) as “Pflanze ausdauernd ..., Wurzelstock holzig, kriechend, verzweigt” (perennial plant ..., root stock wooden, creeping, and branched).

What happens to the primary root of *Inula*? What happens to the tap root of *Potentilla*? The underground systems appear static. Such growth and developmental progress requires explanation. However, our results show a dynamic, and rather different, underground development in these two species.

Potentilla inclinata

The cotyledons develop above ground. Soon, a leaf rosette appears (Fig. 2). The weight of this small rosette bends the hypocotyl (Fig. 2A), and in this way the leaf rosette is brought down to the soil surface. In the following weeks, hypocotyl and primary root form a tap root (Fig. 2B–D). The tap root thickens and contracts,

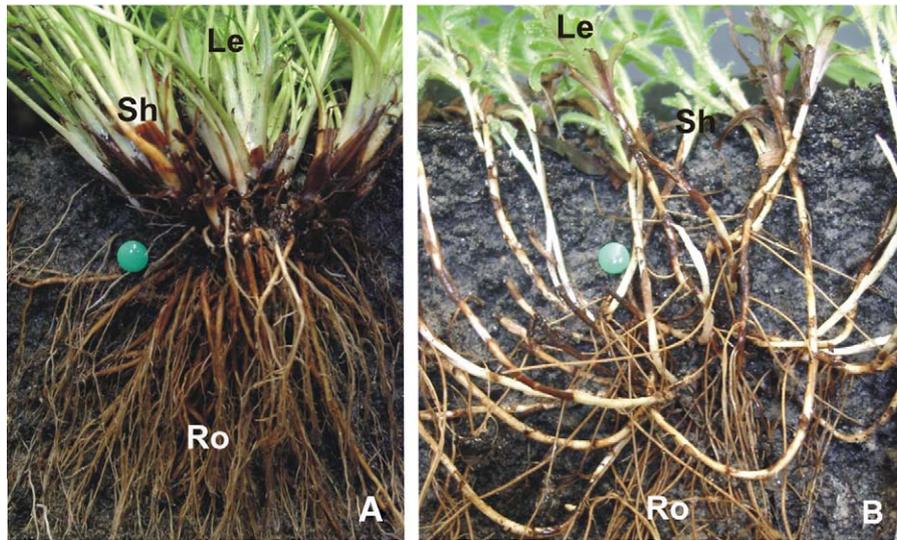


Fig. 1. Subterranean systems of adult (flowering) plants of (A) *Potentilla inclinata*, (B) *Inula ensifolia*. Sh—shoot, Ro—root, Le—leaf.

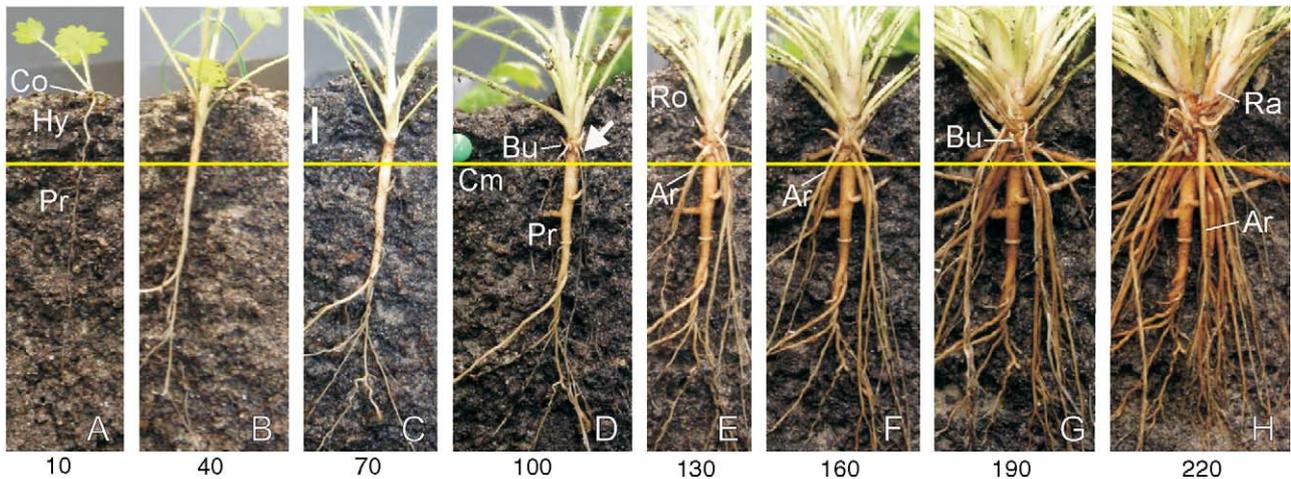


Fig. 2. Time-lapse photography of *Potentilla inclinata*. The number in the lower section of each photo indicates the time of examination after germination in days. The yellow line represents the control mark (starting position of the seed). The bar represents 10 mm. Ar—adventitious roots, Bu—bud, Cm—control mark, Co—cotyledon, Hy—hypocotyl, Pr—primary root, Ra—ramet (new leaf rosette), Ro—rosette. The arrow in (D) points to the first adventitious roots.

so pulling the leaf rosette into a depth of 10 mm (see Fig. 2E). The amount of downward movement found varied from 6 to 22 mm (average 13 ± 6 mm, $n = 12$ plants). During the downward movement (Fig. 2B–E) cotyledons and first leaves wither, and the tap root turns into a typical turnip. The outdoor plants reached the turnip stage (Fig. 2E, F) in autumn, from then on, development was interrupted until spring. Indoors, plants continued their development without interruption.

Further development shows that the root system changes from a typical tap root system (“allorhizy”) to a fibrous root system (“secondary monorhizy”). Adventitious roots appear at the leaf rosette after approx. 100 days of development (Fig. 2D). The number of roots increases over the following months (Fig. 2F–I). The

roots thicken, and, finally, a typical fibrous root system substitutes the turnip (Fig. 2H). This change in root morphology is accompanied by plant cloning. Cotyledon buds and basal rosette leaf buds start their development after approx. 100 days (Fig. 2D). Several buds develop to new plant rosettes (see Fig. 2G and H). No runners exist. The rosettes stay close together. After approx. 310 days (Fig. 1A) the rosettes are still connected. However, all have individual adventitious roots.

Inula ensifolia

The cotyledons develop above ground. Then a leaf rosette appears, which bends the hypocotyl downwards

(Fig. 3A and B). Together with the leaf rosette, adventitious roots develop at the shoot base (Fig. 3C and D). No progress to tap root appears. On the contrary, the increasing number of adventitious roots creates a fibrous root system, and after approx. 130 days, the primary root is completely replaced (Fig. 3F). The leaf rosette is constantly pulled down by contraction of the adventitious roots (cf. in Fig. 3B–G, the rosette base with the control line). After 160 days, the basis of the leaf rosette has reached a depth of approx. 25 mm (Fig. 3G). At this depth shoot basis and renewal buds have reached a safe position to endure their first winter. The amount of downward movement varies from 20 to 40 mm (average 26 ± 11 mm, $n = 10$ plants). During the downward movement, the cotyledons and the first leaves wither (see Fig. 3D). The axis of the leaf rosette elongates several centimetres (Fig. 3G and H) and loses most leaves buried in its underground section (Fig. 3I).

The development continues with cloning. Several buds located in the axes of cotyledons and primary leaves grow into runners (Fig. 3G–I). The orientation of the first runners is vertical, later becoming horizontal (see Fig. 3I).

Outdoors, plants reach the cloning stage in autumn, interrupting their development at a stage similar to

Fig. 3G. Indoors, plants continue their development in a similar fashion as the outdoor plants after dormancy. Ramets reach the soil surface and form new above-ground shoots (Fig. 4A). At this stage, cloning becomes conspicuous. Groups of buds from the runners start growing horizontally into new runners, which soon reach a length of several centimetres (Fig. 4B). Later, buds of first and second generation runners share into this cloning process (see Fig. 4C). Finally, reiteration leads to a multipartite shoot system (see Fig. 1). All runners develop adventitious roots and become independent in their nutrition uptake. However, one year after germination all shoots are still connected.

Discussion

“Plants possessing geophilous organ systems to survive at least one unfavourable season (dry summer, cold winter) in the soil” (Pütz and Sukkau, 2002): This definition includes the categories “cryptophyte” and “hemicryptophyte” (Raunkiaer, 1934). Raunkiaer used mainly the position of the innovation buds to differentiate life forms. However, several studies found a subterranean position of innovation buds in many

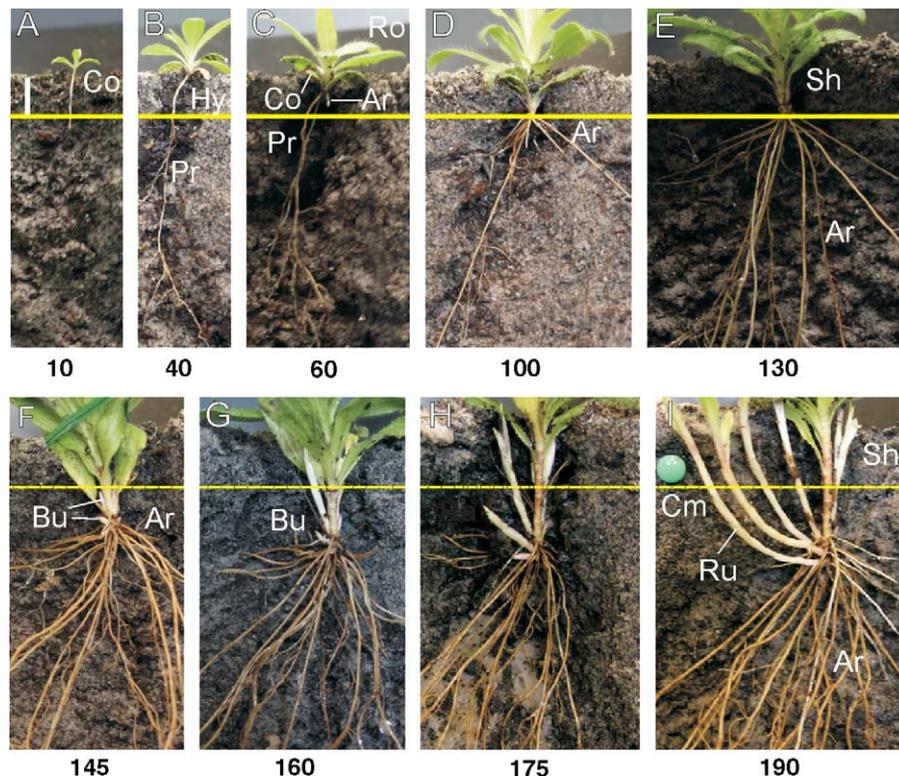


Fig. 3. Time-lapse photography of the development of *Inula ensifolia*. First part: establishment, survival, and innovation. The number in the lower section of each photo indicates the time of examination after germination in days. The yellow line represents the position of the control mark. The bar represents 10 mm. Ar—adventitious roots, Bu—bud, Cm—control mark, Co—cotyledon, Hy—hypocotyl, Pr—primary root, Ro—rosette, Ru—runner, Sh—shoot.



Fig. 4. Time-lapse photography of underground development of *Inula ensifolia*. *Second part: cloning, and vegetative dispersal.* Development into a phalanx clonal plant (Stöcklin, 1992). The number in the lower section of each photo indicates the time of examination after germination in days. The bar represents 10mm. Ar—adventitious roots, Cm—control mark, Ru—runner.

typical “hemicryptophytes” (Gluth and Pütz, 2001 for *Mirabilis jalapa*, compare also Pütz and Sukkau, 2002; Sukkau and Pütz, 2001).

I. ensifolia again demonstrates these difficulties of typological classification. In the first survival phase, the innovation buds are positioned below the soil surface (see Fig. 3F and G). Later, cloning and dispersal by shoot runners occur (Fig. 4). Reiteration buds are below the soil surface, but some shoots are very close to the soil surface (Figs. 4C and 1B). The subterranean system of *I. ensifolia* is multifunctional. A differentiation based only on bud position oversimplifies the situation. The young plant is a cryptophyte (Fig. 3G). The adult plant is a perennial clonal plant, neither a hemicryptophyte nor a cryptophyte.

Subterranean systems of perennials are a complex of organs, their structural components following functional necessities (‘plant construction’, Kaplan and Cooke, 1996; Pütz and Schmidt, 1999; Vandvik and Birks, 2002). Our TLP examinations enable us to observe the underground progress from the seedling stage to the stage of an adult subterranean system, enabling us to describe many formally unknown details, such as the transition from a turnip to a secondary fibrous root system in *P. inclinata*, or the gradual development of the runner system in *I. ensifolia*. TLP examinations allow an uninterrupted documentation of how growth proceeds, the accomplishment of different functions, and the observation of underground kinetics.

In short, growth dynamics follow a three-step progress: (A) establishment of the seedling, (B) survival of an unfavourable season and holding the site occupied, and (C) cloning in the following seasons, combined with vegetative dispersal, fragmentation, and individualism. Moreover, these “three steps of progress” (Fig. 5) include the vertical depth regulation of innovation buds, and the horizontal separation of reiteration buds. Thus, the “three steps of progress” provide a fundamental background for acquiring an overall understanding of subterranean plant behaviour. Thorough studies at the organismic level, for example by Brock et al. (2000) in *Trifolium repens*, can be transferred to our three steps of growth progress. The three main steps merely span variable amounts of time.

The *first step* of progress toward a geophilous system does not include any seed dispersal and germination. Especially the first step of progress indicates establishment of the germinated seedling which is characterised by vertical movement of the plant. In fact, depth regulation of seedling position is a well-known feature. In some cases, leaf elongation brings the innovation buds into a safe soil depth (cf. e.g., Rimbach, 1897, for *Allium ursinum*; Galil, 1983, for *Ixiolirion tataricum*; Pütz and Sukkau, 1995, for *Pancreaticum maritimum*). In many other cases, root and hypocotyl contraction are responsible for the movement (see Pütz, 1996, 2002). *P. inclinata* and *I. ensifolia* exhibit contraction phenomena during seedling establishment. It is interesting to note that in most dicots external contraction features are missing (as is known as, e.g., shrinkage of the root surface in monocots). Therefore, contraction phenomena in dicots are only visible by anatomical studies (e.g. Stevenson, 1980; Zamski et al., 1983), observation of moving processes by TLP (see Figs. 1 and 2), or ink marks (Rimbach, 1926, 1929). Contraction phenomena in seedlings may be a common feature in higher plants, but are a general feature in Apiaceae (Pütz and Sukkau, 2002).

Seedling establishment is often supposed to be rare in clonal plants. Does this signify that the first step in the progress to subterranean systems is less important from

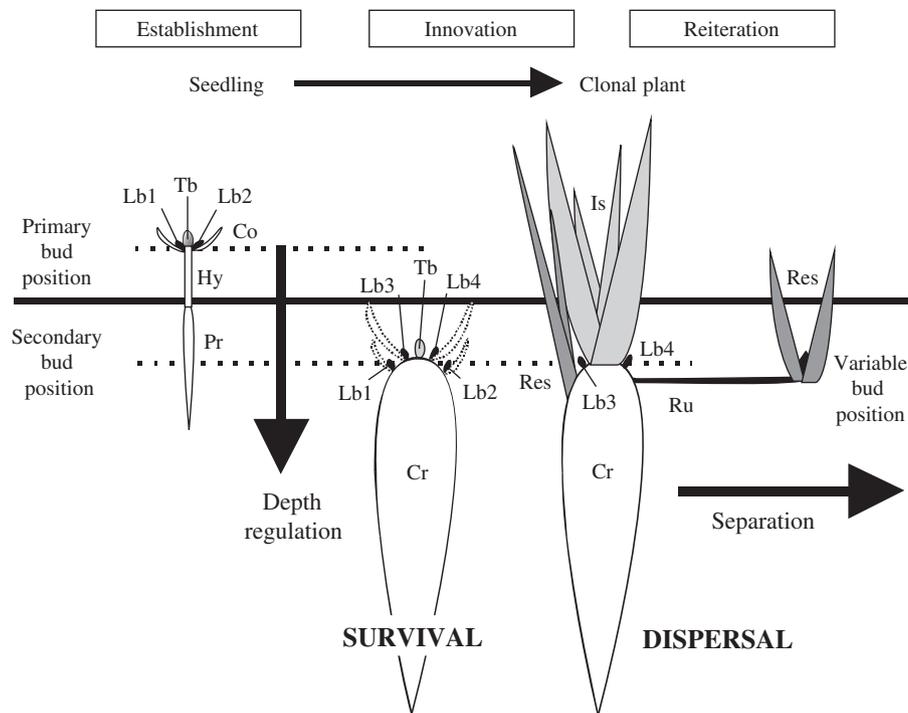


Fig. 5. General pattern of growth progress from a seedling to a clonal plant. The main functions of subterranean systems are survival, and dispersal. During establishment, a kinetic phase of depth regulation brings the renewal bud into a safe soil position. After dormancy follows innovation. During reiteration, a second kinetic phase occurs, which is important for horizontal dispersal of the ramets. Cr—cryptocorm (storing), Co—cotyledon, Hy—hypocotyl, Is—innovation shot, Lb—bud of rosette leaf, Pr—primary root, Res—reiteration shoot, Ru—runner, Tb—terminal bud.

an ecological point of view? Eckert (2001) sees no empirical evidence to support this. Forbis (2003) reports lots of seedlings of clonal plants in an alpine ecosystem. Of course, there exist species where seedlings are rarely encountered. “In *Agave macroantha*, the establishment of seedlings and bulbils is a rare event that possibly only occurs under nurse plants in many years, while ground-level cloning is highly effective as a propagation mechanism” (Arizaga and Ezcurra, 2002). In contrast, Winkler and Stöcklin (2002) describe a mixture of “clonal growth and reproduction by seeds” in the reproductive strategies of *Hieracium pilosella*, a combination which seems necessary for both preserving the habitat and conquering new sites (see also Chaloupecká and Lepš, 2004; Eggert, 1992; Zhou et al., 2003). Clearly, a close examination of seedling establishment and of the behaviour of seedlings under different external parameters (e.g., Brock and Tilbrook, 2000; Brock et al., 2000; Meyer and Schmid, 1999) have an overall importance in order to understand the structure of subterranean systems.

The second step (underground progress, survival at the site), requires at least one innovation bud for next year’s sprouting, and, of course, nutrient storage. The fulfillment of these functions increases the diversity at the organographical level. Features are: (1) organs for depth regulation of the system (or parts of the system),

(2) location of nutrient storage, (3) position of innovation buds in the system, (4) position of reiteration buds, and (5) facilities for horizontal separation. Such organographical changes are not included in Fig. 5, because they often result in a great variation. For example, manifold definitions for underground plant organs by location of storage exist (see Krumbiegel, 2002; Lampe, 1999). Furthermore, often more than one type of storage and sprouting patterns develop during the progress of subterranean growth. In *Trifolium repens*, the tap root stage of the seedling is followed by development of a stolon system (Brock et al., 2000). *P. inclinata* has a typical turnip to survive the first unfavourable season. Thereafter, older plants change to a fibrous root system and to a storing complex at the shoot base (“pleiocorm” according to Meusel, 1951).

The third step of progress toward a geophilous system consists of cloning, vegetative dispersal, fragmentation, and individualisation. This step of progress describes the maximally versatile programme of progress. It should be mentioned that not all perennials possess the general tendency of cloning, dispersal, and fragmentation. However, in most cases organographical variation and ecological potential increase during these processes. Reiteration buds grow out, while the subterranean systems divide into fragments and new individuals (ramets, clones) appear. Investigations of e.g. Bell and

Tomlinson (1980), Van Kleunen and Fischer (2003), Meyer and Schmid (1999), Sachs (2001), Stöcklin (1992), Yu et al. (2001), and Oborny and Kun (2001) focus on this step. However, detailed observations show that our knowledge of these processes is still very incomplete. Even our data for just two species already showed unexpected aspects. Nearly every detailed examination of subterranean growth patterns will add to our knowledge of these long neglected processes (e.g., dispersal of daughter bulbs in *Oxalis pes-caprae* (Pütz, 1994); separation of secondary taproots in *Anthriscus sylvestris* (Pütz and Sukkau, 2002; Sukkau and Pütz, 2001)). Furthermore, soil moisture, light intensity, nutrient availability, or neighbourhood relations result in a bewildering, only initially understood, plasticity of clonal plants (e.g. Chen et al., 2004; Humphrey and Pyke, 2001; Luo and Dong, 2002; Münzbergová et al., 2005; Yu and Dong, 2003).

The final step in the growth progress in particular, the kinetic aspect, exhibits considerable diversity. Ramet dispersal from the mother plant is a horizontal moving process. In many cases, this movement results from stolon growth (Dong et al., 2002; Fischer et al., 2004; Pütz, 1998; Troll, 1937; Winkler and Stöcklin, 2002). Many species use the existing root system for separation and the formation of root suckers (Nadeau et al., 1991; Rauh, 1937). In some cases, contraction phenomena result in horizontal movement and separation (e.g., *Triteleia hyacinthina* (Pütz, 1991); *Oxalis pes-caprae* (Pütz, 1994)).

A conclusive review about the vast diversity realised at species level is in progress. The individual form of the three-step growth process is a major asset for the establishment and survival of a species. For example, Song et al. (2002) and Song and Dong (2002) correlated the diversity of plant species with phalanx and guerrilla strategies in a transect in North-East China. Plants with guerrilla strategy are positively correlated with steppe habitats, while plants with phalanx strategy are negatively correlated. In a complex habitat, analysis must focus not only the life-form or special strategies of clonal plants. Consideration must also be given to the overall “survival strategy”, including generative dispersal, seedling establishment, keeping occupied the site, cloning, vegetative dispersal, fragmentation, and individualisation. Consideration of these aspects in combination will give us a deeper understanding of plant interaction and, finally, of the functioning of plant communities.

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References

- Arizaga, S., Ezcurra, E., 2002. Propagation mechanisms in *Agave macroacantha* (Agavaceae), a tropical arid-land succulent rosette. *Am. J. Bot.* 89, 632–641.
- Bell, A.D., Tomlinson, P.B., 1980. Adaptive architecture in rhizomatous plants. *Bot. J. Linn. Soc.* 80, 125–160.
- Brock, J.L., Tilbrook, J.C., 2000. Effect of cultivar of white clover on plant morphology during the establishment of mixed pastures under sheep grazing. *N. Z. J. Agric. Res.* 43, 335–343.
- Brock, J.L., Albrecht, K.A., Tilbrook, J.C., Hay, M.J.M., 2000. Morphology of white clover during development from seed to clonal populations in grazed pastures. *J. Agric. Sci.* 135, 103–111.
- Chaloupecká, E., Lepš, J., 2004. Equivalence of competitor effects and tradeoff between vegetative multiplication and generative reproduction: case study with *Lychnis flos-cuculi* and *Myosotis nemorosa*. *Flora* 199, 157–167.
- Chen, J.-S., Yu, D., Liu, Q., Dong, M., 2004. Clonal integration of the stoloniferous herb *Fragaria vesca* from different altitudes in Southwest China. *Flora* 199, 342–350.
- Dong, M., Dearing, H.J., Werger, M.J.A., 2002. Root and shoot plasticity of the stoloniferous herb *Ajuga reptans* L. planted in a heterogeneous environment. *Flora* 197, 37–46.
- Eckert, C.G., 2001. The loss of sex in clonal plants. *Evol. Ecol.* 15, 501–520.
- Eggert, A., 1992. Dry matter economy and reproduction of a temperate forest spring geophyte, *Allium ursinum*. *Ecography* 15, 45–55.
- Fischer, M., Van Kleunen, M., Schmid, B., 2004. Experimental life-history evolution: selection on growth form and its plasticity in an clonal plant. *J. Evol. Biol.* 17, 331–341.
- Forbis, T.A., 2003. Seedling demography in an alpine ecosystem. *Am. J. Bot.* 90, 1197–1206.
- Galil, J., 1958. Physiological studies on the development of contractile roots in geophytes. *Bull. Res. Council. Isr.* 6, 223–236.
- Galil, J., 1980. Kinetics of bulbous plants. *Endeavour* 5, 15–20.
- Galil, J., 1981. Morpho-ecological studies on geophilic plants. Vegetative dispersal of *Gynandris sisyrinchium* L. *Isr. J. Bot.* 30, 165–172.
- Galil, J., 1983. Morpho-ecological studies of lowering in the seedling of the geophyte *Ixiolirion tataricum* (Pall.) Herb. *New Phytol.* 143, 143–150.
- Gerstberger, P., 2003. 26. *Potentilla*. In: Weber, H.E. (Ed.), Gustav Hegi. *Illustrierte Flora von Mitteleuropa*, Band IV Teil 2C. Spermatophyta: Angiospermae; Dicotyledones 2(4). Rosaceae (Rosengewächse). Paul Parey, Berlin, pp. 109–205.

- Gluth, H., Pütz, N., 2001. Zur unterirdischen Entwicklung und Überdauerung der Wunderblume *Mirabilis jalapa* L. (Nyctaginaceae). *Wulfenia* 8, 15–26.
- Halevy, A.H., 1986. The induction of contractile roots in *Gladiolus grandiflorus*. *Planta* 167, 94–100.
- Humphrey, L.D., Pyke, D.A., 2001. Ramet spacing of *Elymus lanceolatus* (thickspike wheatgrass) in response to neighbour density. *Can. J. Bot.* 79, 1122–1126.
- Jernstedt, J., 1984. Seedling growth and root contraction in the soap plant, *Chlorogalum pomeridianum* (Liliaceae). *Amer. J. Bot.* 71, 69–75.
- Kaplan, D.R., Cooke, T.J., 1996. The genius of Wilhelm Hofmeister: the origin of causal-analytical research in plant development. *Am. J. Bot.* 83, 1647–1660.
- Krumbiegel, A., 2002. Morphologie der vegetativen Organe (außer Blätter). *Schriftenr. Naturkunde (Bundesamt Naturschutz, Bonn)* 38, 93–118.
- Lampe, von M., 1999. Vorschlag zur Bezeichnung der Innovations- und Überdauerungsorgane bei den terrestrischen Stauden Zentraleuropas. *Biol. Pflanz.* 71, 335–367.
- Luo, X.G., Dong, M., 2002. Architectural plasticity in response to soil moisture in the stoloniferous herb, *Duchesnea indica*. *Acta Bot. Sin.* 44, 97–100.
- Meusel, H., 1951. Die Bedeutung der Wuchsform für die Entwicklung des natürlichen Systems der Pflanzen. *Feddes Repert.* 54, 137–172.
- Meyer, A.H., Schmid, B., 1999. Experimental demography of rhizome populations of establishing clones of *Solidago altissima*. *J. Ecol.* 87, 42–54.
- Münzbergová, Z., Křivánek, M., Bucharová, A., Jukličková, V., Herben, T., 2005. Ramet performance in two tussock plants—do the tussock-level parameters matter? *Flora* 200, 275–284.
- Nadeau, L.B., Dale, M.R.T., Kig, J.R., 1991. The development of spatial pattern in shoots of *Linaria vulgaris* (Scrophulariaceae) growing on fallow land or in barley crop. *Can. J. Bot.* 69, 2539–2544.
- Oborny, B., Kun, A., 2001. Fragmentation of clones: how does it influence dispersal and competitive ability? *Evol. Ecol.* 15, 319–346.
- Pütz, N., 1991. Die Zugbewegungstypen bei den Monokotylen. *Bot. Jahrb. Syst.* 112, 347–364.
- Pütz, N., 1993. Underground plant movement. I. The bulb of *Nothoscordum inodorum* (Alliaceae). *Bot. Acta* 106, 338–343.
- Pütz, N., 1994. Vegetative spreading of *Oxalis pes-caprae*. *Plant Syst. Evol.* 191, 57–67.
- Pütz, N., 1996. Underground plant movement. IV. Observance of the behaviour of some bulbs with special regard to the induction of root contraction. *Flora* 191, 313–319.
- Pütz, N., 1998. Underground plant movement. V. Contractile root tubers and their importance to the mobility of *Hemerocallis fulva* L. (Hemerocallidaceae). *Int. J. Plant Sci.* 159, 23–30.
- Pütz, N., 2002. Contractile roots. In: Waisel, A., Eshel, I., Kafkafi, Y. (Eds.), *Plant Root: The Hidden Half*. Marcel Dekker, New York, pp. 975–987.
- Pütz, N., Schmidt, K.H.A., 1999. ‘Underground plant mobility’ and ‘dispersal of diaspores.’ Two exemplary case studies for useful examinations of functional morphology (plant construction). *Syst. Geogr. Plant* 68, 39–50.
- Pütz, N., Sukkau, I., 1995. Comparative examination of the moving process in monocot and dicot seedlings using the example *Lapeirousia laxa* (Iridiaceae) and *Foeniculum vulgare* (Apiaceae). *Feddes Repert.* 106, 475–481.
- Pütz, N., Sukkau, I., 2002. Seedling establishment, bud movement, and subterranean diversity of subterranean systems in Apiaceae. *Flora* 197, 385–393.
- Pütz, N., Pieper, J., Froebe, H.A., 1997. The induction of contractile root activity in *Sauromatum guttatum* (Araceae). *Bot. Acta* 110, 49–54.
- Rauh, W., 1937. Die Bildung von Hypokotyl- und Wurzelsprossen und ihre Bedeutung für die Wuchsformen der Pflanzen. *Nova Act. Leopold.* 4, 1–137.
- Raunkiaer, C., 1934. *The Life Form of Plants and Statistical Plant Geography*. Clarendon Press, Oxford.
- Rimbach, A., 1897. Lebensverhältnisse des *Allium ursinum*. *Ber. Dtsch. Bot. Ges.* 15, 248–252.
- Rimbach, A., 1898. Die kontraktilen Wurzeln und ihre Tätigkeit. *Beitr. Wiss. Bot.* 2, 1–26.
- Rimbach, A., 1926. Über Verkürzung von Stengeln. *Ber. Dtsch. Bot. Ges.* 44, 335–338.
- Rimbach, A., 1929. Die Verbreitung der Wurzelverkürzung im Pflanzenreich. *Ber. Dtsch. Bot. Ges.* 47, 22–31.
- Sachs, T., 2001. Developmental processes and the evolution of plant clonality. *Evol. Ecol.* 15, 485–500.
- Song, M.H., Dong, M., 2002. Clonal plants and plant species diversity in wetland ecosystems in China. *J. Veg. Sci.* 13, 237–244.
- Song, M.H., Dong, M., Jiang, G.M., 2002. Importance of clonal plants and plant species diversity in the Northeast China Transect. *Ecol. Res.* 17, 705–716.
- Stevenson, D.W., 1980. Observations on root and stem contraction in cycads (Cycadales) with special reference to *Zamia pumila* L. *Bot. J. Linn. Soc.* 81, 275–281.
- Stöcklin, J., 1992. Umwelt, Morphologie und Wachstumsmuster klonaler Pflanzen—eine Übersicht. *Bot. Helv.* 102, 3–21.
- Sukkau, I., Pütz, N., 2001. Beobachtungen zur geophilen Überlebensstrategie bei *Anthriscus sylvestris* und *Aegopodium podagraria* (Apiaceae). *Wulfenia* 8, 81–93.
- Troll, W., 1937. *Vergleichende Morphologie der höheren Pflanzen, I. Vegetationsorgane*. Borntraeger, Berlin.
- Vandvik, V., Birks, H.J.B., 2002. Pattern and process in Norwegian upland grasslands: a functional analysis. *J. Veg. Sci.* 13, 123–134.
- Van Kleunen, M., Fischer, M., 2003. Effects of four generations of density-dependent selection on life history traits and their plasticity in a clonally propagated plant. *J. Evol. Biol.* 16, 474–484.
- Wagenitz, G., 1979. *Compositae I: Allgemeiner Teil, Eupatorium-Achillea*. In: Conert, H.J., Hamann, U., Schultze-Motel, G., Wagenitz, G. (Eds.), *Gustav Hegi, Illustrierte Flora von Mitteleuropa*. Parey, Berlin.
- Winkler, E., Stöcklin, J., 2002. Sexual and vegetative reproduction of *Hieracium pilosella* L. under competition and disturbance: a grid-based simulation model. *Ann. Bot.* 89, 525–536.

- Yu, F.H., Dong, M., 2003. Effect of light intensity and nutrient availability on clonal growth and clonal morphology of the stoloniferous herb *Halerpestes ruthenica*. *Acta Bot. Sin.* 45, 408–416.
- Yu, F.H., Chen, Y.F., Dong, M., 2001. Clonal integration enhances survival and performance of *Potentilla anserina*, suffering from partial sand burial on Ordos plateau, China. *Evol. Ecol.* 15, 303–318.
- Zamski, E., Ucko, U., Koller, D., 1983. The mechanism of root contraction in *Gymnarrhena micranatha*, a desert plant. *New Phytol.* 95, 29–35.
- Zhou, Z.H., Miwa, M., Nara, K., Wu, B.Y., Nakaya, H., Lian, C.L., Miyashita, N., Oishi, R., Maruta, E., Hogetsu, T., 2003. Patch establishment and development of a clonal plant, *Polygonum cuspidatum*, on Mount Fuji. *Mol. Ecol.* 12, 1361–1373.