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Research article

Intermediate growth forms as a model for the study of plant clonality functioning: an example with root sprouters

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Abstract. In this contribution we want to show that growth forms intermediate between non-clonal and clonal plants can be used to ask questions about the functional ecology of clonality. We discuss this idea on plants sprouting adventitiously from roots and accomplishing clonal growth via root spacers. Based on extensive literature dealing with growth forms of root sprouting plants, we characterise forms functionally intermediate between clonal root-sprouters and non-clonal plants. We delimit them according to their potential ability to form adventitious shoots and horizontal roots. By reviewing experimental work with root-sprouters, we identify the most important triggering factors and developmental constraints influencing these intermediate forms: plant age, life-history mode and life-history stage. Using this information we ask questions about the importance of root sprouting in (1) conditions of unpredictable disturbance, where root-sprouting ability may be viewed as a tool for vegetative regeneration, and in (2) temporarily and spatially heterogeneous environment, where foraging by roots may serve as a way of exploiting patchy resources.

Key words: adventitious buds on roots, biennials, bud bank, plant injury, reiteration

Introduction

Sachs (2002) has recently postulated that developmental processes distinguishing clonal plants from their non-clonal relatives might be understood as rearrangements and quantitative changes of overall morphology. Since more than one change is required for a non-clonal plant to become clonal, intermediate forms possessing only an incomplete set of clonal properties must also have certain ecological advantages allowing them to exist and to be ‘stepping stones’ on the pathway from a non-clonal to a clonal plant. Sachs (2002) showed that such intermediate forms really could be found using the example of plants with stem spacers (i.e., new ramets of these plants are established by a plagiotropic shoot whose apex turns upwards and forms an erect stem at some distance from the mother plant). He distinguished branch differentiation, development of erect axes and formation of shoot-borne roots as developmental processes steering for clonality. Furthermore, he discussed developmental mechanisms operating during plant morphogenesis, and outlined possibilities for further research of functional aspects of clonality based on stem spacers by studying the intermediate forms.

Inspired by Sachs' paper, we want to do the same intellectual exercise with plants whose ramets are not formed at the apex of a horizontal stem (stoloniferous or rhizomatous plants), but along horizontal roots (root-sprouters). As root sprouting is of polyphyletic origin (Groff and Kaplan, 1988; Klimešová and Klimeš, in prep.) and we have no data mapping the evolutionary pathways at least not in certain genera of root sprouting plants differing in architecture, we will not follow the attempt of Sachs to interpret the intermediate forms evolutionarily. Functionally intermediate forms allow us to study functional aspects of clonal vs. non-clonal growth, and also to ask questions about the adaptability of clonal growth in root-sprouters. Our goal is to integrate our knowledge about the growth forms and ecology of root sprouting plants and to build up hypotheses testable by using functionally intermediate growth forms. We try to achieve this goal in several steps: first, we describe what root sprouting is; second, we outline functionally intermediate growth forms; third, we review triggering mechanisms of root sprouting in different growth forms.

Root sprouting

In addition to buds formed during embryogenesis and in the axils of leaves, buds can also be found at other locations on the plant body: on leaves, stems, hypocotyl and roots (Kerstetter and Hake, 1997). Because of their unusual location apart from leaf axils they are called adventitious (Groff and Kaplan, 1988). While axillary buds develop exogenously during normal shoot growth from the apical meristem, adventitious buds often need special stimuli to be formed endogenously from more or less differentiated tissues (Esau, 1965). The ability to form adventitious buds on roots is limited to less than 10% of the Central European flora (Klimešová and Klimeš, in prep.). Formation of adventitious buds on roots is a typical feature of some plant families (Podostemataceae) or genera (*Euphorbia, Linaria, Rorippa*). On the other hand, it is unknown in Monocotyledons except Orchidaceae (Rauh, 1937). A typical clonal root sprouting plant has long horizontal roots creeping close to the soil surface, root sprouting is spontaneous, and the area covered by a genet may be enormous (e.g., aspen clones – Brodie *et al.,* 1995). Except for this typical form, many others also exist, either with less extensive clonal growth or with only facultative formation of root sprouts.

Review of growth form classifications

In spite of the small number of root sprouting plants, the diversity of their growth forms is enormous and has been subjected to detailed morphological study. Similar analyses covering all rhizomatous plants do not exist.

The first descriptions of root-sprouters originate from the middle of 19th century (Irmisch, 1857, 1859; Reichardt, 1857). Already Wittrock (1884) listed 138 root sprouting species in Europe (including cultivated plants). Also the first attempt to typify root-borne shoots according to their biological significance dates back to Wittrock (1884). He recognised three types of root sprouting: (1) additive – root-shoots arise during normal plant ontogeny but are not necessary to complete the plant's life cycle; (2) necessary – root-shoots are necessary for flowering or over-wintering of the plant; (3) regenerative – root-shoots arise only after injury to a plant (Fig. 1).

A next growth-form analysis of root-sprouters was published by Rauh (1937). After detailed studies of many species, Rauh elaborated a growth form system, in which the main groups were classified as obligate root-sprouters, facultative root-sprouters and regenerative root-sprouters. These three categories correspond to some extent with the three types proposed by Wittrock (1884). Exceptions are plants which have a flowering main shoot and regularly sprout from roots. They are classified as additive root-sprouters after Wittrock and obligatory root-sprouters after Rauh (e.g., *Rumex acetosella*).

Moreover, Rauh's groups were further divided based on the fate of the main shoot (flowering vs. non-flowering) and the localisation of adventitious shoots (hypocotyl, main root, lateral roots) (Fig. 1). However, Rauh (1937) not only classified root-sprouters and described their ontogenetic development, but also noticed a correlation between the development of the main (primary) shoot and the spontaneity of root sprouting. Rauh outlined a series of growth forms of related taxa, ranging from species with adventitious buds restricted to the hypocotyl and arising only facultatively and with a potentially flowering main shoot (*Euphorbia helioscopia*, *E. segetalis*), through a type in which root-sprouts grow spontaneously from the hypocotyl and the main root, and in which the main shoot flowers (*E. gerardiana*), to species with spontaneous root sprouting from the main root and with non-flowering main shoots (*E. amygdaloides*) and eventually, to species with non-flowering main shoots and vigorous root sprouting from horizontal roots (*E. cyparissias* and *E. esula*) (Fig. 2). Rauh described a similar spectrum of growth forms also in the genus *Linaria* and related species. Whereas species with facultative root sprouting restricted to the main root and hypocotyl are short-lived, obligate root-sprouters with non-flowering main shoots and horizontal roots ('Wurzel Ausläufer') are perennial in the two genera mentioned. Even though Rauh

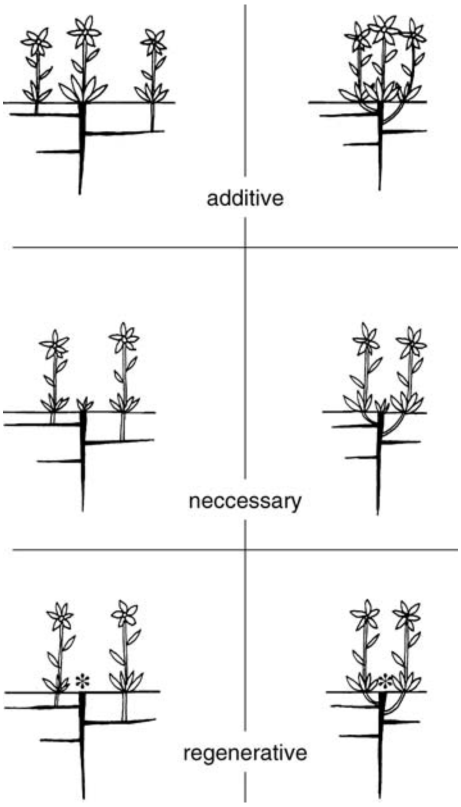

Figure 1. The role of adventitious sprouting in the life of plants. Left icons – adventitious shoots are formed on horizontal roots; right icons – adventitious shoots are formed on main root and/or hypocotyl (according to Rauh, 1937); additive – flowering and over-wintering of plants is not dependent on root-sprouting; necessary – flowering and over-wintering of plants is dependent on root-sprouting; regenerative – root-sprouting is triggered by injury to plant body; asterisk – injury (according to Wittrock, 1884).

indicated the respective forms by such adjectives as 'basic type' or 'derived type', he did not interpret them explicitly in evolutionary terms.

Replacement of the main shoot by adventitious shoots inspired Aeschimann and Bocquet (1980) to a new classification of root-sprouters. Their classification is based on symmetry with the concept of allorhizy vs. homorhizy (Groff and Kaplan, 1988). They distinguished plants with either a primary root or a primary shoot only as representatives of allorhizy and allocauly, respectively. Plants with the main root substituted by shoot-borne roots (adventitious roots) were classified as representatives of homorhizy, and plants with the main shoot substituted by root-borne shoots (adventitious shoots) as representatives of homocauly. They further distinguished 'accidentelles' (i.e., accidental), 'sup-

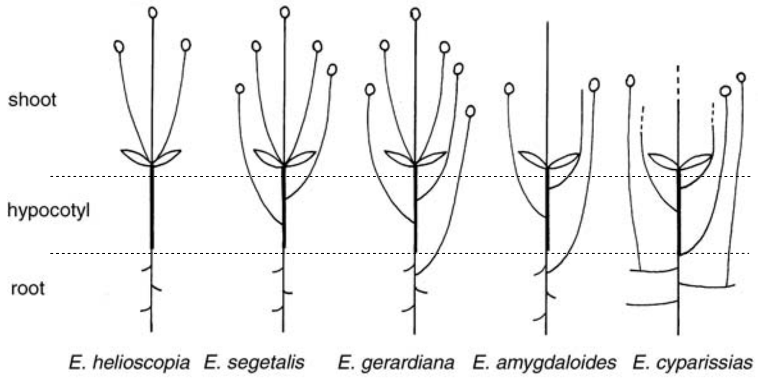

Figure 2. Schema of growth of root sprouting members of the genus *Euphorbia*. Flowering shoots are marked by circles (according to Rauh, 1937). For details see text.

plémentaires' (i.e., additional) and 'vicariantes' (i.e., replacing) adventitious roots and shoots (Fig. 1). These categories are similar to Wittrock's classification of root-sprouters. A shortcoming of the classification is the implicit exclusion of the possibility that one plant can possess adventitious shoots and adventitious roots at the same time.

The most complex system of relations between root and shoot systems in vascular plants (not only in root-sprouters) was proposed by Groff and Kaplan (1988). They distinguished four 'Structural classes'. I – The plant has only a primary shoot system and primary root system, clonal growth is limited to vertical fragmentation. II – The plant forms adventitious roots, clonality is attained by fragmentation of the shoot system. III – The plant forms adventitious shoots, clonality is attained by fragmentation of the root system. IV – The plant forms both adventitious shoots and roots (Fig. 3), therefore three possibilities for clonal growth exist: (a) only the shoot system fragmentises, (b) only the root system fragmentises, or (c) both the root and shoot system fragmentise (Fig. 3). This classification covers all principal types of clonal and non-clonal plants. A shortcoming of this classification is that not all species capable of producing adventitious shoots or roots, or both, really display clonal growth (Rauh, 1937; Sachs, 2002). Moreover, it is not taken into consideration that clonal growth can be achieved by normal growth or by reiteration (*sensu* Hallé *et al*., 1978).

Agnes Arber with her theory of partial shoot (Arber, 1930, 1941) stays apart from the positions of the German typology school represented by Rauh (1937), Aeschimann and Bocquet (1980) and Groff and Kaplan (1988). She views the ability of roots of some species to form adventitious shoots as a proof of the shoot and root not being distinct morphological categories, i.e., the potentiality

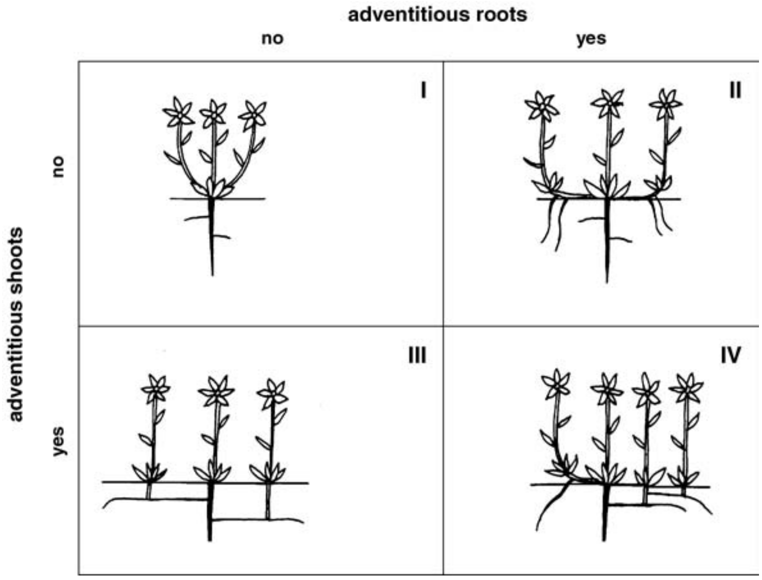

Figure 3. Participation of adventitious roots and adventitious shoots in structural classes (I–IV) by Groff and Kaplan (1988). Structural classes embody possible ways how to achieve clonal growth.

to behave as a shoot lies dormant within the character of a root. This hypothesis of dynamic plant morphology has no phylogenetic implications (Classen-Bockhoff, 2001). This developmental point of view has the advantage of no boundaries being laid across the process, which is without doubt continuous. On the other hand, typology gives us a useful tool for the description of the observed pattern.

Functionally intermediate growth form

We delimited the following attributes necessary for extensive clonal growth: formation of root-borne shoots and plagiotropic growth of roots. On the other hand, formation of adventitious (shoot-borne) roots seems to be unnecessary because indefinitely growing lateral roots starting to decay from their older parts may serve extensive clonality well (Groff and Kaplan, 1988) (Fig. 3). Limited performance of the attributes is found in plants that potentially sprout from roots and thus potentially grow clonally to some extent. Those plants may be classified as regenerative and additional root-sprouters after Wittrock (1884) and facultative and regenerative root-sprouters after Rauh (1937), and Aeschimann and Bocquet (1980).

We may find potential root-sprouters among all life-forms. While perennial potential root-sprouters are able to regenerate from root buds after injury and then continue the usual iterative growth, short-living monocarpic species (e.g., *Rorippa palustris, Oenothera biennis, Barbarea vulgaris*) often change their growth form or life history (prolongation of life span, prolongation of juvenile phase, polycarpy, extensive growth of lateral roots or adventitious roots) by triggering root sprouting (Dubard, 1903; Rauh, 1937; Kott, 1963; Klimešová, 2003).

As root systems are very plastic in relation to soil quality, horizontal roots may be observed in many plants both with and without root sprouting (Kutschera and Lichtenegger, 1992). However, it is reported that root sprouting may be a triggering factor for horizontal growth of roots. According to Wehsarg (1954) *Knautia arvensis* and *Centaurea scabiosa* growing on arable land may lose all aboveground parts and even the upper parts of their belowground organs by ploughing. After such severe injury the plants regenerate from their fleshy main roots and produce several adventitious shoots compensating for the lost parts. On underground parts of adventitious stems, adventitious roots arise during the growing season, and from them adventitious shoots regrow. Root-borne shoots translocate assimilates preferentially to the apical end of the adventitious mother root (see also Troll, 1941; Fykse, 1974). This means that the original main root successively loses its dominant function and a unitary plant turns into a clonal root sprouter (Wehsarg, 1954). A similar trend can be observed in the short-lived herbs *B. vulgaris* (Kott, 1963) and *Cirsium arvense* (Wehsarg, 1954). The plants start, after injury, to produce adventitious buds on their horizontal roots and support their lateral growth. But this is possible only in wet soil, where the plants have a richly branched main root. In dry or heavy soil the main root is poorly branched, and regeneration may therefore be restricted.

Factors triggering root sprouting

The most studied factors triggering root sprouting are external factors such as disturbance (injury to plant body) and nutrient level. The interactions of these external factors with ontogeny are less examined, but they also play an important role in the ability of a plant to sprout adventitiously from roots.

External factors

Disturbance. Root sprouting is conditioned or stimulated by disturbance of plant integrity in the majority of plants (Peterson, 1975). Most trees do not begin sprouting from roots until the primary trunk has been injured (Del Tredici, 2001). Removal of or injury to aboveground plant parts facilitates and often enables the formation of new root buds, or break their dormancy and also facilitate growth of new root-borne shoots (Rauh, 1937; Peterson, 1975; Del Tredici, 2001; Martínková *et al*., 2004a, b). Examples of such disturbances are defoliation, decapitation, cutting of branches or removal of all aboveground plant parts. For example, McIntyre (1972) found that decapitation of lateral branches of the perennial herb *E. esula* promotes elongation and growth of root buds. Horvath (1998, 1999) showed that leaves and growing meristems (apical or axillary buds) of the same species prevented root buds from breaking quiescence, or reduced the growth of root buds. In an experiment with juvenile plants of the short-lived herb *Rorippa palustris,* it was found that the number of initiated adventitious buds on roots was markedly enhanced by injury. On the other hand, the severity of injury (defoliation vs. removal of all leaves and stem parts) does not play any role in root-sprouting of this species (Martínková *et al*., 2004b). This implies that *R. palustris* produces preformed adventitious buds on its roots, but does not resprout from them until a plant is injured. Rauh (1937) found the same strategy in *Geranium sanguineum* and *Rumex sanguineus*. On the other hand, *Oenothera biennis* forms root buds and releases new root-borne shoots almost exclusively after injury (Martínková *et al*., 2004a), even though these buds are not formed directly on the callus tissue as in some other species, e.g., *Trifolium alpestre, Centaurea scabiosa* (Rauh, 1937).

Injury to the plant body is the most essential factor triggering root-sprouting regardless of the fact that the extent of injury necessary for activation or formation of adventitious buds on roots varies among species.

Nutrient level. Mineral nutrition has an important effect on the growth of root sprouting plants (Peterson, 1975). Higher nutrient levels support bud formation, break down bud dormancy and facilitate growth of root-borne shoots in perennial species (Peterson, 1975). However, an opposite effect was also found: the number of adventitious buds on roots of *Chondrilla juncea* was not affected by the nutrient level, but the growth of new shoots was supported by low nutrient levels (Kefford and Caso, 1972). According to a study by McIntyre and Hunter (1975) on another perennial weed of arable land, *Cirsium arvense*, root buds are initiated more frequently on plants growing at lower nutrient levels than at higher ones. Nadeau and Van den Born (1990) found no effect of nitrogen addition on the number of emerged root buds. However, the majority of these buds remained dormant under these conditions and new shoots were developed from established root buds more frequently in environments with a higher nutrient availability (McIntyre and Hunter, 1975). Similarly, Klimeš and Klimešová (1999a) found that nutrition stress facilitated the formation of root buds in *Rumex acetosella*, but their growth and transition to shoots was enhanced at higher nutrient levels. Studies on *Rorippa palustris* (Martínková *et al.*, 2004a, b) showed that the number of adventitious buds formed on roots was not affected by nutrition level, but a higher nutrient level supported the release of buds and growth of new root-borne shoots.

The relationship between nutrient level and root sprouting is still uncertain, but it seems that both regenerative growth after disturbance and transition of root buds into shoots are facilitated at higher nutrient levels. The number of buds is either not affected by nutrient level, or supported by nutrient shortage.

Internal factors

Plant age. Information on the relationship between plant age and root-sprouting ability is very scarce, but it is obvious that root sprouting following injury is dependent on plant age (Martínková *et al.*, 2004b). Very young seedlings are unable to form adventitious buds on their roots and to sprout, because the ability to root-sprout is connected with sufficient assimilation and the presence of activated meristem tissue (Esau, 1965; Peterson, 1975). Evetts and Burnside (1972) found that injured juveniles of *Asclepias syriaca* were able to sprout at the age of three weeks. Some injured juveniles of the short-lived herbs *Rorippa palustris* and *Barbarea vulgaris* were capable of root-sprouting at the age of four weeks, and 100% regeneration occurred already in six-week old juveniles of these species (Martínková *et al.*, 2004b). However, all adventitious buds formed on roots were used for growth of new shoots after disturbance at this age, thus no dormant root buds were left in place for a possible later disturbance (Martínková *et al.*, 2004b). In contrast to this, eight-week old plants of *R. palustris* save some adventitious buds on their roots for possible later disturbance as an insurance for faster regrowth (Martínková *et al.*, 2004b). It also seems that plant age is more important for the root-sprouting ability than plant size. Injured plants of *R. palustris* reached comparable values of plant size characteristics (number of leaves, rosette diameter, etc.) in two different experiments. Nevertheless, younger plants were not as successful in root sprouting after injury as older plants (Martínková *et al.*, 2004b).

Life-history mode. The life-history mode of *Rorippa palustris* is determined by the time of germination; germination from April to June results in an annual life-history mode, while winter annual plants germinate later in the growing season (Sosnová, 2003). In a study by Martínková *et al.* (2004a), both life-history modes of this species were artificially induced by manipulating with day length in a growth chamber experiment. The root-sprouting ability was independent of the life-history mode of the experimental plants, only the extent of regeneration was influenced by it (Martínková *et al.*, 2004a). In a garden experiment with sequentially sown cohorts of *R. palustris*, Sosnová (2003) found that plants behaving as (summer) annuals regenerated more successfully than plants in winter annual mode. According to these studies, it seems that injury to the plant body is more disadvantageous for plants in the winter annual life-history mode than for plants in the (summer) annual life-history mode. No study was found that would compare the root sprouting ability of short-lived plants with that of perennial plants.

Life-history stage. The poorest root sprouting of perennial species occurs at the time of flowering (Peterson, 1975). Dubard (1903) and Rauh (1937) noticed that the biennials *Alliaria officinalis* and *Bryonia dioica* were able to sprout from roots only at the end of the first growing season, and the short-lived herb *Oenothera biennis* was only in vegetative stage (rosette). According to a more recent study (Martínková *et al*., 2004a), *O. biennis* regenerates from roots also in the generative phase (fruiting stem), but less successfully than in the vegetative stage. The same result was found for the short-lived perennial *Barbarea vulgaris* (Martínková *et al*., in prep.). Moreover, flowering plants of *O. biennis* and *B. vulgaris* regenerate more successfully than plants setting seeds (Martínková *et al*., 2004a, b; Martínková *et al*., in prep.). In some woody species sprouting ability increases with size to reach a maximum at adult stage. In other species, however, sprouting is common in juveniles whereas adults are unable to resprout (Del Tredici, 2001). This pattern of resprouting ability throughout a plant's life can be interpreted as a consequence of reserve accumulation capability and reserve allocation to growth or reproduction (Dubard, 1903; Chapin *et al.,* 1990; Bellingham and Sparrow, 2000; Bond and Midgley, 2001). On the other hand, no seasonal pattern was found in the presence of root buds in different times of the year in *Cirsium arvense* (McAllister and Haderlie, 1985).

In perennial plants, resprouting from roots often starts in the second year of their life, when the main shoot dies (Rauh, 1937). However, young plants of *Epilobium angustifolium* are able to sprout in the first year of their life if they are severely injured (Klimešová pers. obs.).

The observed relationships between root sprouting and ontogeny are not only direct but also more complicated, and all possible interactions of the known triggering factors together should be taken into account.

Conclusions

The proportion of root-sprouters differ among growth forms. It was found to be the highest of all growth forms in biennials and trees (Klimešová and Klimeš, 2003). These forms do not possess clonal growth organs of stem origin (such as stolons or rhizomes) or a below-ground bud bank. Even root-sprouting perennial herbs usually do not posses any other organ that could be used for clonal growth (Irmisch, 1857; Klimeš and Klimešová, 1999b). It seems that the evolution of clonality via root spacers was probably not only independent of, but also alternative to that mediated by stem spacers (rhizomes and stolons).

Facultative root-sprouters, especially biennials, seem to suit our demands for functionally intermediate forms between a unitary plant and a clonally growing root-sprouter. As injury is the main triggering factor of root sprouting in short-lived perennials, we cannot exclude the possibility that potential sprouting represents an adaptation to unpredictable disturbance. In experiments, where clonality is manipulated by severe injury to the plant body, we cannot, unfortunately, separate the advantage of bud bank formation from an initiation of clonal growth. An important question is, if root-sprouting biennials differ from non-sprouting ones in their allocation to growth, flowering and storage. Alternatively, one may ask whether root-sprouting biennials, after being injured at a specific age and ontogenetical stage of development, change allocation between structures of vegetative vs. generative regeneration. It follows from studies on ontogenetical constraints on potential root sprouting that switching from exclusive investment into seed formation to the investment into vegetative growth declines with progressive exhaustion of reserves allocated to fruits.

Another promising direction of research can be seen in the manipulation with root sprouting by temporal heterogeneity in nutrient availability. Three main factors, enhanced formation of adventitious buds due to nutrient shortage, vigorous sprouting due to nutrient addition, and root proliferation in rich soil patches, may be responsible for opportunistic growth of root sprouting plants. Root sprouting is a form of foraging, since roots must grow for other reasons, so it could be an extremely efficient way of searching the environment for the best locations (see also Sachs, 2002). This strategy may be advantageous in nutrient-limited habitats, such as xeric grasslands, where a relatively high proportion of root-sprouters is found (Klimešová and Klimeš, in prep.).

We can conclude that clonality via root spacers may be viewed as a way of vegetative regeneration. We cannot exclude clonality attained by reiteration, because injury to plant body in habitats with unpredictable disturbance may become an important stimulus for repeated occurrence of intermediate forms between clonal and non-clonal plants in such habitats. On the other hand, obligate root-sprouters among perennial plants may beregarded as typical representatives of a 'sit and wait' strategy, as theypossess prerequisites for foraging in temporarily heterogeneous environments.

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