

Letters

Root-sprouting in myco-heterotrophic plants: prepackaged symbioses or overcoming meristem limitation?

Many plants spread by clonal growth. In most cases this is achieved using underground stems (e.g. rhizomes or stolons) which bear axillary buds at their nodes. New, potentially independent shoots (ramets) establish from these axillary buds. Clonal reproduction by the formation of adventitious shoots from roots is also possible (Groff & Kaplan, 1988) but is much less common. Only *c.* 10% of the species of the Central European flora are capable of forming adventitious buds on roots and sprout from them (Klimešová & Martíková, 2004), as particular hormonal and developmental barriers have to be overcome. Moreover, root sprouting plays different roles in the life cycle and growth form of individual plants (Wittrock, 1884; Rauh, 1937). In some, this is a necessary component towards completing their life cycle, for others it is an additional trait to 'normal' axillary stem branching, while in some this is a regenerative trait triggered by injury.

Necessary root sprouting may be found in very ecologically distinct groups; parasites, myco-heterotrophic plants and river weeds (Podostemaceae). In myco-heterotrophic plants, Domínguez *et al.* (2006) discovered the formation of root propagules capable of adventitious sprouting, which soon detach from the parent plant and probably provide a clonal growth mode assuring the proper fungal symbiont to its vegetative offspring – 'prepackaged symbioses'. By clonal multiplication, a genet will produce more shoots and consequently more seeds leaving more sexual progeny, despite high seed and seedling mortality. Adventitious sprouting has been reported in several myco-heterotrophic species by several authors (Leake, 1994); however, the infection of propagules has not been studied and requires further examination. I wish to offer another explanation for root sprouting in myco-heterotrophs; this is not an alternative but rather a complementary idea to that of Domínguez *et al.* (2006). The Central European flora will be used as an example. This flora contains a relatively small number of myco-heterotrophic plants, but the clonal growth modes of the plants are well known (Klimeš *et al.*, 1997; Klimešová & Klimeš, 2006).

Dicotyledonous myco-heterotrophs and parasites in the Central European flora are characterised by a reduction of the primary stem in early ontogeny to such an extent that no axillary buds develop and plant growth is totally dependent on adventitious bud formation on the root or hypocotyle. Ecologically, the primary shoot is redundant in early ontogeny, as the plants draw carbon from hosts (parasites) or symbionts (myco-heterotrophic plants) below ground. The primary shoot may be lost in evolution in the case of overcoming meristem limitations by producing adventitious shoots later in ontogeny, merely to ensure sexual reproduction (full myco-heterotrophs; *sensu* Bidartondo, 2005) or for both sexual reproduction and carbon autonomy (initial myco-heterotrophs). For example, a myco-heterotrophic plant from the Ericaceae family, *Monotropa hypopithys*, germinates in the presence of a symbiont (Leake *et al.*, 2004) with the embryo developing only a root pole. Roots supported by fungi form adventitious buds endogenously from the pericycle, close to the lateral roots (in stage 4 of germination according to Leake *et al.*, 2004). Next-year buds sprout into adventitious shoots and, after flowering, die down to the parental root. Sprouting in the following year is again dependent on the formation of adventitious buds (Rauh, 1937). The plant perennates via the root system and adventitious sprouting results in clonal growth. No specialised root propagules are formed; however, new adventitious shoots arise from the infected root system. Therefore, no special means are needed to spread the symbiont into daughter plants as they remain connected to the parental root, which survives *c.* 3 yr (Beijerinck, 1887).

Another example is provided by representatives of the former Pyrolaceae family, which are only represented in Central Europe by photosynthetic plants (initial myco-heterotrophs). *Moneses uniflora* shows a similar ontogeny to *Monotropa*; however, its roots are thin and show a considerable lateral spread, while the aerial shoots survive several years of flowering (polycyclic shoots) (Irmisch, 1855; Rauh, 1937). Seedlings of *Orthilia secunda* germinate in a similar fashion to the preceding species: only by the root pole of the embryo (the same holds for all members of Ericaceae family listed in Table 1; Bobrov, 2004), and produce one adventitious shoot, which develops axillary buds for growth of a thin rhizome from which polycyclic shoots arise. Root sprouting from adventitious roots is also possible in the later stages of ontogeny (Irmisch, 1855); however, its contribution to clonal multiplication has never been quantified.

Unlike the dicotyledonous representatives of myco-heterotrophs in the Central European flora, orchids develop a primary shoot, form rhizomes on which there are axillary meristems for sprouting (Leake *et al.*, 2004) and, moreover,

Table 1 List of mycoheterotrophic root-sprouters from the Central European flora with sources of morphological description

Species	Family	Source
<i>Botrychium lunaria</i> (L.) SW.	Ophioglossaceae	13†
<i>Botrychium virginianum</i> (L.) SW.	Ophioglossaceae	13†
<i>Ophioglossum vulgatum</i> L.	Ophioglossaceae	3, 4, 12*, 15*
<i>Cephalanthera alba</i> (CRTZ.) SIMONKAI.	Orchidaceae	20
<i>Cephalanthera longifolia</i> (L.) FRITSCH	Orchidaceae	16
<i>Cephalanthera rubra</i> (L.) RICH.	Orchidaceae	12, 20*
<i>Epipactis atrorubens</i> (HOFFM.) BESSER	Orchidaceae	5†
<i>Epipactis microphylla</i> SWARTZ.	Orchidaceae	11†
<i>Goodyera repens</i> R. BR.	Orchidaceae	20†
<i>Limodorum abortivum</i> (L.) SW.	Orchidaceae	20*
<i>Listera cordata</i> (L.) R. BR.	Orchidaceae	12*, 17, 20*
<i>Listera ovata</i> (L.) R. BR.	Orchidaceae	17, 20*
<i>Neottia nidus-avis</i> (L.) RICH.	Orchidaceae	3, 12*, 20*
<i>Spiranthes aestivalis</i> RICH.	Orchidaceae	3†
<i>Spiranthes autumnalis</i> RICH.	Orchidaceae	3†
<i>Monotropa hypopitys</i> L.	Ericaceae	3*, 6, 9, 12*
<i>Monotropa hypophegea</i> WALLR.	Ericaceae	13†
<i>Chimaphila umbellata</i> (L.) BARTON	Ericaceae	7†
<i>Moneses uniflora</i> (L.) A. GRAY	Ericaceae	2, 6, 8*, 12*, 18, 19
<i>Orthilia secunda</i> (L.) HOUSE	Ericaceae	1, 6, 8*, 12*, 14*, 18
<i>Pyrola chlorantha</i> SW.	Ericaceae	8, 10

*Picture available; †, only notice, without description.

¹Bagdasarova (1990); ²Bagdasarova & Vakhrameeva (1990); ³Beijerinck (1887); ⁴Filin (1995); ⁵Summerhayes (1968); ⁶Grevillius and Kirchner (1925); ⁷Holm (1925); ⁸Irmisch (1855); ⁹Irmisch (1857); ¹⁰Irmisch (1859); ¹¹Penzig (1921, 22); ¹²Rauh (1937); ¹³Jäger and Werner (2002); ¹⁴Rysin and Rysina (1987); ¹⁵Troll (1941); ¹⁶Vakhrameeva *et al.* (1996); ¹⁷Varligina (1995); ¹⁸Velenovský (1905, 07); ¹⁹Warming (1908); ²⁰Ziegenspeck (1936).

Species printed in bold are fully myco-heterotrophic, others are myco-heterotrophic only in early ontogeny. Other fully myco-heterotrophic plants from the flora (*Corallorhiza trifida* and *Epipogium aphyllum* from Orchideae) have no roots.

sprout adventitiously from roots (see sources in Table 1). They use two modes of clonal growth: while rhizomes are usually perennating for many years and do not spread far laterally, the roots are separated early from the parent plant and, in some species, they provide some lateral growth (Ziegenspeck, 1936; Filin, 1995). In these plants, adventitious sprouting is not necessary for completion of the plant life-cycle, but is an additive trait providing clonal multiplication, similar to the case described by Domínguez *et al.* (2006). An interesting point, however, is that the orchids listed in Table 1 are the only root-sprouting monocots in Central Europe.

The coincidence of mycoheterotrophy and the ability to sprout adventitiously from roots is both ecologically and evolutionarily interesting and cannot be interpreted solely as an ecological adaptation. The role of the fungal symbiont in triggering root sprouting (the possible production of phytohormone-like substances; see Arshad & Frankenberger, 1991; Tsavkelova *et al.*, 2006), or their transport from a green host, has not been ruled out and needs to be taken into account, as it would provide a unifying explanation for the observed pattern. We can even speculate that root sprouting may be a by-product of the hormonal imbalance 'designed' for reversed carbon flow from the fungal symbiont to myco-heterotrophs. Adventitious bud formation is known

to be triggered by a low auxin : cytokinin ratio (Banno *et al.*, 2001), which should be typical for myco-heterotrophs because auxin is produced by mature green and expanding leaves (Sachs, 2005).

Acknowledgements

I am indebted to Keith Edwards for improving my English and to an anonymous reviewer for comments. Support from a Research grant from the Academy of Sciences of the Czech Republic to the Institute of Botany (no. AV0Z60050516) is acknowledged.

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Key words: adventitious buds on roots, bud limitation, clonal growth, Ericaceae, myco-heterotrophic plants, Ophioglossaceae, Orchidaceae.