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ECOLOGY OF (HEMI)PARASITIC PLANTS

Habilitation Thesis

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Abstrakt

Tato habilitační práce se věnuje ekologii parazitických a poloparazitických rostlin. V její první části probírám evoluční ekologii rostlinného parazitismu. Druhů část je zaměřena na ekologii kořenových poloparazitů, které jsou spolu se jmelími největší funkční skupinou parazitických rostlin. Jejich ekologii představuji z mnoha pohledů, od ekofyziologických mechanismů interakce mezi hostitelem a poloparazitem, přes aspekty ekologie společenstev a ekosystémové ekologie, po využití poloparazitů v ekologických aplikacích. Součástí habilitační práce je 10 vědeckých článků, které přispěly k rozvoji poznání ekologie (polo)parazitických rostlin.

Abstract

This thesis deals with the ecology of parasitic and hemiparasitic plants. In its first part, I introduce the evolutionary ecology of plant parasitism. The second part focuses on ecology of root hemiparasites, together with mistletoes the largest functional groups of parasitic plants. I adopt a comprehensive view on their ecology ranging from the ecophysiological mechanisms of the hemiparasite-host interaction to community and ecosystem ecology, including also applications of root-hemiparasites in ecological restoration. The thesis is supplemented by 10 research papers which contributed to understanding (hemi)parasitic plant ecology and evolution.

Acknowledgement

Content

1. Story of losers or winners? Evolutionary ecology of parasitic plants

Most plants are photoautotrophic organisms. Their vital processes depend on carbon from CO_2, energy from light and also water and mineral nutrients. While availability of CO_2 in the air is rarely limiting and can be considered as a condition for plant life, the other three factors are resources available in limited supply. Therefore, they are subject of competition between co-occurring plants. Plants have evolved a number of strategies to facilitate acquisition of these resources. Some of them involve ecological interactions with other organisms. Of these, mutualistic mycorrhizal associations with fungi contributing mineral nutrients in exchange for organic carbon are most common in vascular plants. In fact, most plant species do establish mycorrhizal association, a symbiosis which is likely to have facilitated land colonization by plants (Smith & Read, 2008). Several evolutionary lineages of vascular plants (including e.g. Fabaceae, Cycadales, and a number of Fagales) developed mutualistic symbiosis with (cyano)bacteria, which have ability to fix nitrogen, one of the principal biogenic elements, from the atmosphere (Stevens, 2001; Li *et al.*, 2015). While the strategies mentioned above involve bidirectional exchange of resources, others involve exclusively flows of resources towards plant recipients, i.e. they are purely heterotrophic. Mycoheterotrophy refers to the cases where the balance of the originally mutualistic symbiosis shifted towards the benefit of the plant partner (Merckx, 2013). While most mycoheterotrophs retain photosynthetic ability (partial mycoheterotrophs), several evolutionary lineages are non-green and their carbon nutrition is completely dependent on fungal partner (Selosse & Roy, 2009). Another example includes carnivorous plants which trap and digest animal prey to acquire mineral nutrients, in particular nitrogen (Givnish, 2015). Plant parasitism defined as direct parasitic interaction between plant individuals represents one of the heterotrophic resource-acquisition strategies which contributes not only mineral nutrients but also water and variable amount of organic carbon.

The mechanism of plant parasitism is based on connection between vascular bundles of two plant species – the parasite and the host. This connection is established by a specialized organ called the haustorium which is developed as a modification of roots or stems of parasitic plants. Parasitic plants comprise *ca.* 4500 species, which accounts for 1% of angiosperms (Těšitel, 2016). Parasitism has evolved at least 12 times independently in the angiosperm evolution (Barkman *et al.*, 2007; Naumann *et al.*, 2013). Species diversity is distributed very unevenly among individual evolutionary lineages of parasitic angiosperms. Two largest groups, the Orobanchaceae family and the Santalales order comprise *ca.* 90% of parasitic species while multiple groups (Hydnoraceae, Mitrastemonaceae, Cynomoriaceae and Lennooidae) contain

less than 10 species (Těšitel, 2016). Individual lineages markedly differ also in their estimated phylogenetic age. Santalales are the oldest lineage of extant parasitic plants, origin of which is estimated to early Cretaceous *ca.* 110 Mya (Naumann *et al.*, 2013). By contrast, the youngest transitions to the parasitic strategy were reconstructed in the family Orobanchaceae and the parasitic genus *Cuscuta* of Convolvulaceae. These groups are of late Paleogene age (32 and 35 Mya, respectively) which also indicates the upper boundary of the age of transition to parasitism (Naumann *et al.*, 2013). The uneven species richness of individual parasitic plant lineages was recently related with their phylogenetic age to show that there is little correlation between the two parameters and the non-parasitic sister clades are mostly more species rich than the parasitic lineages (Hardy & Cook, 2012; Naumann *et al.*, 2013). Such pattern would indicate a strongly limited evolutionary potential of parasitic plants, a hypothesis suggested by Hardy & Cook (2012) on the basis of sister-clade comparisons of parasitic and mycoheterotrophic plants. Notable exceptions to this are however the two largest parasitic lineages of Santalales and Orobanchaceae, species richness of which is higher than that of their respective non-parasitic sister clades by several orders of magnitude (Hardy & Cook, 2012). Naumann et al. (2013) postulated an alternative temporal specialization hypothesis (TSH) explaining the evolution of parasitic plants through an assumption that efficiency of parasitic pathways increases in time together with host specificity. This should produce multiple small, specialized and relict groups of highly specialized parasites together with few relatively young, non-specialized and diversified groups. This hypothesis generally seems to fit well with the empirical evidence on phylogenetic age, trophic specialization and species richness of the parasitic angiosperm lineages (Naumann *et al.*, 2013); however there is one important exception. Santalales are the oldest and simultaneously most species-rich group of extant parasitic plants. They display a range of trophic modes ranging from non-parasitic to full heterotrophy (Naumann *et al.*, 2013; Těšitel, 2016) with predominance of photosynthetic hemiparasites. This was also acknowledged by Naumann et al. (2013) who however tried to incorporate existence of Santalales into their hypothesis by pointing on existence of small specialized groups within the clade. In contrast to these previous studies investigating exclusively the evolutionary patterns, I am convinced that the complex evolutionary pattern of parasitic angiosperms may only be understood through examination of the extensive functional diversity relating to their physiology (dependence on host species, ability to withdraw resources), life forms, ecological interactions and also geographical distribution.

The physiological functioning of individual parasitic plant species can be described by a set of functional traits (Těšitel, 2016). Ability of photosynthesis indicates autonomy in carbon acquisition and varies from fully functional to completely missing photosynthesis. Closely associated with photosynthetic ability is the anatomical structure of the host-parasite contact in the haustoria. Some parasites access host xylem only while others take up resources from both xylem and phloem (Hibberd & Jeschke, 2001). Non-photosynthetic species mostly access both types of vascular bundles due to the need of abundant carbon nutrition provided by phloem (Irving & Cameron, 2009); however, this is not a strict rule due to existence of xylem-only feeding holoparasitic plants (Těšitel & Tesařová, 2013; Světlíková *et al.*, 2015; Těšitel, 2016). Other important traits relate to germination, which may be either induced by host presence or not, and establishment of the initial connection to the host by primary (terminal) haustoria or secondary (lateral) haustoria. Location of haustoria on roots or stems of the host determine life forms of parasitic plants, that is root or stem-parasites. The most advanced parasitic species however form extensive endophytic structures which may extend from root to shoot (Heide-Jørgensen, 2008). As a result, the distinction between root and stem parasites is not relevant in their case. Four functional groups of parasitic plants may thus be distinguished in the basis of the functional traits mentioned above – root-hemiparasites, root-holoparasites, stem parasites and endophytic parasites (Těšitel, 2016).

These functional groups make sense from morphological, physiological and ontogenetic points of view. However differences between some of them lack distinctness from the perspective of ecological interactions, resource acquisition and use. For instance, there is little difference in the ecological interactions between root-holoparasites and endophytic parasites since both are (typically) completely dependent on host for carbon and do not compete with the host for light. Therefore, I introduce here a scheme displaying major adaptive evolutionary steps which can be traced in the parasitic plants evolution (Fig. 1). Each of the steps involves an evolutionary innovation addressing a major ecological constraint limiting occurrence/abundance of its predecessors which did not display such innovation.
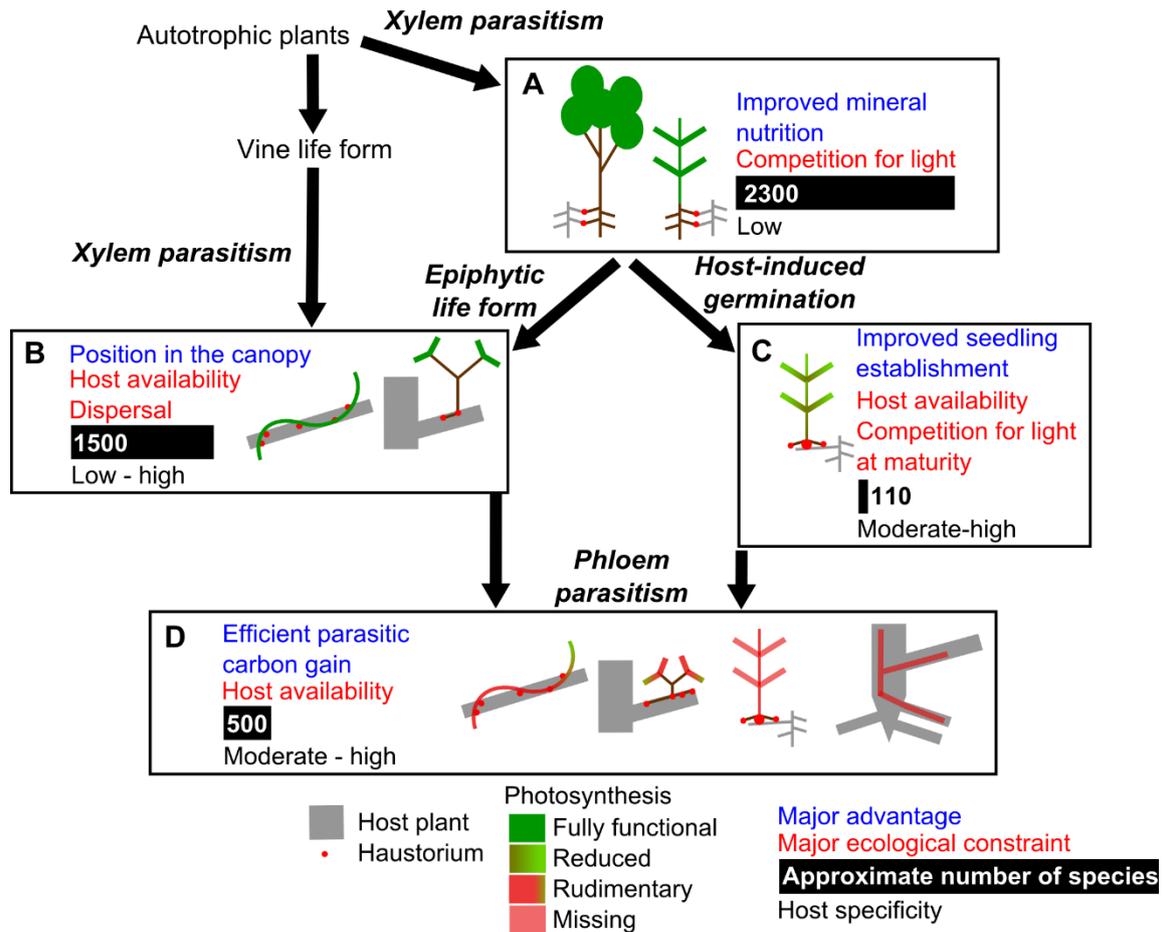
Fig. 1. Scheme of the evolution of parasitism in the angiosperms. Major evolutionary innovations facilitating parasitic resource acquisition are indicated by arrows. Rectangles encapsulate principal evolutionary steps which comprise plants differing in their physiological functioning, resource acquisition strategies and ecological interactions. Major ecological constraints overcome (i.e. advantages) and associated with respective evolutionary steps are provided together with the number of species and estimate of predominant host specificity. Illustration of photosynthetic ability refers to the state of a majority of species; some important exceptions, e.g. non-photosynthetic *Lathraea* in C are commented in the text. Note, that phloem continuity in the haustoria may be difficult to demonstrate in some less-well studied groups (Cynomoriaceae, Mirrastemonaceae, Hydnoraceae); as a result, their placement in C or D is not resolved to date.

Development of xylem connection to the host represents the first step in the evolution of plant parasitism (Fig. 1A). This provides access to the xylem-borne resources, namely mineral nutrients, water and also a limited amount of carbon (Hibberd & Jeschke, 2001; Irving & Cameron, 2009; Těšitel *et al.*, 2010a; Jiang *et al.*, 2010; Bell & Adams, 2011). This root-hemiparasitic strategy is characteristic of most Orbanchaceae, Krameriaceae and a substantial part of Santales. Access to host xylem largely facilitates mineral nutrition of the parasitic plants

providing a great competitive advantage over non-parasitic species. This competitive advantage is however realized through own photosynthetic activity, rate of which is strongly increased by nutrients obtained heterotrophically (Těšitel *et al.*, 2015b). Therefore, the parasitic plants which display only this initial albeit crucial evolutionary innovation retain photosynthetic activity mostly in a fully functional state. As a result of this dependency on own photosynthesis, they are affected by competition for light from both the host species and other co-occurring species in the community. In fact, competition for light is the principal constraint limiting their performance (Fig. 1A; Matthies, 1995; Fibich *et al.* 2010; Těšitel *et al.*, 2011, 2013).

To address this constraint, some of these parasitic plants (hemiparasitic Santalales) evolved epiphytic mistletoe life form. Others (genus *Cassytha* of Lauraceae; also *Cuscuta* of Convolvulaceae, all extant species of which access host phloem) underwent the transition to parasitic xylem-feeding strategy from autotrophic epiphytic vine life forms. Either evolutionary pathway resulted in a photosynthetic xylem-feeding epiphyte (Fig. 1B), which addresses much of the constraint imposed by competition for light. Occurrence of such parasitic plants is however dependent on availability of suitable host species which are large and long-living enough to support the epiphytes. Dispersal is another important issue for mistletoes germinating on host branches (Mathiasen *et al.*, 2008). By contrast *Cassytha* germinates on the ground which however means that competition for light can still affect its establishment.

The effects of competition for light have most detrimental effects on the seedlings of the root-hemiparasitic plants (Fig. 1A; Těšitel *et al.* 2011) restricting their regeneration niche (Grubb, 1977). To address the seedling establishment constraint, multiple species evolved initiation of seed germination by presence of host root associated with a holoparasitic-seedling stage (Fig. 1C). Such strategy, intermediate between hemi- and holo- parasitism (Westwood *et al.*, 2010), is typical for a number of genera of Orobanchaceae, namely *Striga*, *Alectra*, *Tozzia* and perennial species of *Rhynchocorys*. The xylem-only connection to the host provides only a limited amount of carbon, which requires a transition to own photosynthesis either early in the subsequent ontogeny (*Striga*, *Alectra*) or a slow-growing, long-lasting underground non-green stage (*Tozzia, Rhynchocorys*). Most of these plants still produce green shoots which allow transformation of their mineral-nutrition benefits into offspring production by photosynthesis. The importance of the autotrophic pathway for generative-reproduction organs has indeed been demonstrated directly in *Striga* (Santos-Izquierdo *et al.*, 2008) or may be indirectly deduced from green shoots which are always fertile in *Tozzia* and *Rhynchocorys* (Těšitel *et al.*, 2010b). The evolutionary stability of their photosynthetic activity (albeit frequently lowered; Graves *et*

al., 1992) is thus secured by a reduction of fitness in eventual non-green mutants. Still, xylem only-feeding species of the genus *Lathraea* growing in closed-canopy forest lost photosynthesis probably as a result of minimal contribution of own photosythesis in the shady environment and lack of necessity to quickly complete its life cycle in a stable environment with plentiful resources contributed by long-living hosts. Moreover, the long-living xylem only-feeding holoparasite stage relies for carbon nutrition of xylem sap with low concentration of carbon. Sufficient carbon can be obtained only together with excessive amount of water, which cannot be discarded by transpiration. These species therefore feature specialized hydathode trichomes on scales of leaf origin covering their rhizomes, which actively excrete excess water (Ziegler, 1955; Renaudin & Garrigues, 1967; Weber, 1975; Těšitel & Tesařová, 2013; Světlíková *et al.*, 2015). This active process requires energy, which further decreases physiological efficiency of these parasitic plants.

The constraints related to carbon nutrition in xylem-only feeding hemiparasites, i.e. sensitivity to competition for light or the need for highly specialized and inefficient physiology, were addressed by the evolution of connection to host phloem in the haustoria (Fig. 1D). Phloem sap is rich in organic carbon providing sufficient nutrition to support both growth and reproduction of phloem feeding parasites which become practically independent of light conditions. None of the phloem-feeding parasitic plants displays functional photosynthesis which would contribute substantial proportion of its carbon budget. This indicates that photosynthetic ability is quickly lost after evolution of phloem connection due to genetic drift acting upon plastid genome devastating functionality of genes involved in synthesis of photosynthetic apparatus (Wicke *et al.*, 2013). While plastid genome itself is retained in most phloem feeding non-green species, recent research discovered that it may be eventually lost (Molina *et al.*, 2014). Most of the phloem-feeding holoparasitic lineages indeed lost the ability to photosynthesis in its entirety (Balanophoraceae, Cytinaceae, Cytinaceae, Lenooidae, most holoparasitic Orobanchaceae). By contrast, some species retain rudimentary photosynthetic ability. This is the case of the genus *Cuscuta*, where most species retain photosynthesis contributing to lipid synthesis which is crucial for offspring production as lipids constitute the seed reserves but their concentration in host phloem sap is low (McNeal *et al.*, 2007). The photosynthetic activity may also facilitate foraging for the host in the pre-attachment phase of *Cuscuta* seedlings (Švubová *et al.*, 2013). Similarly, in dwarf mistletoes (genus *Arceuthobium* of Viscaceae, Santalales), rudimentary photosynthesis may play role in seed production (Miller & Tocher, 1975) and establishment on host branches may be greatly facilitated by energy

coming from photosynthesis of green endosperm present in all mistletoes (Heide-Jørgensen, 2008; Nickrent & García, 2009).

The efficient carbon nutrition allowed phloem-feeding parasites to colonize and thrive in habitats with conditions unfavourable for autotrophic plant life or largely exploitative, resource-wasting hemiparasitic strategy. These include e.g. dark forest understory or arid places, where holoparasitic phloem-feeding plants indeed frequently occur (Těšitel, 2016).. Given the efficiency of carbon nutrition by phloem feeding, an apparent question also arises: why did not all parasitic plants evolve this nutritional mode to avoid constraints imposed by competition for light? It seems that establishment of phloem contact is much more complicated compared to xylem contact – phloem is a living tissue and at least certain level of specific interaction with the host to facilitate transfer of the resources from host phloem to the parasite (Irving & Cameron, 2009). The higher specialization of phloem-feeding compared to xylem only-feeding haustoria implies also greater hosts specificity. This means that most of the phloem-feeding parasites are limited by host availability, which rarely limits distribution of xylem-feeding hemiparasites (in particular root-hemiparasites). Exemplified by the case of Orobanchaceae, horizontal gene transfer between host and parasite (which was documented in multiple phloem-feeding lineages; (Davis & Xi, 2015) has recently been suggested to play an important role in the evolution of phloem-feeding ability (Yang *et al.*, 2016). However, horizontal gene transfers are still rather rare events; obtaining the set of genes necessary for phloem-contact establishment may thus require substantial amount of time even on the evolutionary time scale. The evolution towards greater efficiency of heterotrophic carbon acquisition may moreover be hindered by the contrast between the hemiparasitic and holoparasitic strategies. Despite variable gain of host-derived carbon in the hemiparasites (Těšitel *et al.*, 2010a; Bell & Adams, 2011), they capitalize the benefits of their parasitism via own photosynthesis (Těšitel *et al.*, 2015b). Switching to holoparasitism means that the principal benefits of hemiparasitism, i.e. low-cost yet abundant mineral nutrition and water supply, are lost as holoparasites cannot benefit from their elevated availability.

Looking back to the evolutionary pattern of parasitic angiosperms, what can be concluded about the theories aiming at its explanation by the hypotheses on ecological limitation of parasitic plant diversification (Hardy & Cook, 2012) or temporal specialization (Naumann *et al.*, 2013)? Both of these hypotheses have a structure of universal laws of nature, which are however exercised on the evolutionary history. Such approach has been demonstrated inadequate from the philosophical perspective (Popper, 1957; Taleb, 2007). Moreover, both of

these hypotheses are refuted by data available, most notably by the existence Santalales, a species-rich group containing mostly relatively non-specialized root- or stem-hemiparasitic plants (Těšitel, 2016). If the two proposed hypotheses are wrong and universal theory describing the evolution of plant parasitism is impossible, what can I offer instead? I propose an interpretation of the evolutionary pathways of individual parasitic plant lineages and their similarities.

Clearly, we can identify a number of small and functionally homogeneous lineages in the parasitic plants on the one hand and two highly successful species-rich and a functionally diverse groups on the other. This contrast will further increase when we consider their geographic distributions. The small holoparasitic lineages typically have a limited geographic distribution. The geographic ranges of Cytinaceae, Apodanthaceae and Mitrastemonaceae are also disjunct (Heide-Jørgensen, 2008), which indeed indicates their relict origin. By contrast, the two most successful lineages, Santalales and Orobanchaceae, have global distributions, which also applies for the genus *Cuscuta* (Heide-Jørgensen, 2008). These three groups represent an omnipresent component of principal terrestrial ecosystems worldwide. Root-hemiparasitic Santalales have been successful in both tropical woody and open temperate vegetation (Fig. 2A) , while Loranthaceae and Viscaceae, two independently evolved mistletoe lineages within the order (Nickrent *et al.*, 2010), colonized predominantly forest, savanna and other woody vegetation from the tropics to the temperate (Fig. 2B; Heide-Jørgensen, 2008). Root-parasitic Orobanchaceae have been highly successful in the open vegetation and diversified in both temperate and tropical grassland biomes (Fig. 2C,D; McNeal *et al.*, 2013). Hemiparasitic species of both Santalales and Orobanchaceae are moreover recognized as keystone species with profound effects on the communities and ecosystems, where they occur (Press, 1998; Watson, 2001, 2009, 2016; Phoenix & Press, 2004). Similarly, the genus *Cuscuta* has a global geographic distribution and its species were demonstrated to play a keystone role in structuring plant communities (Callaway & Pennings, 1996, 1998). Considering the other groups, species

of the genus *Cassytha* are mostly restricted to Australia but *C. filiformis* has a remarkable pantropic distribution (Heide-Jørgensen, 2008). In their Australian homeland, the *Cassytha*
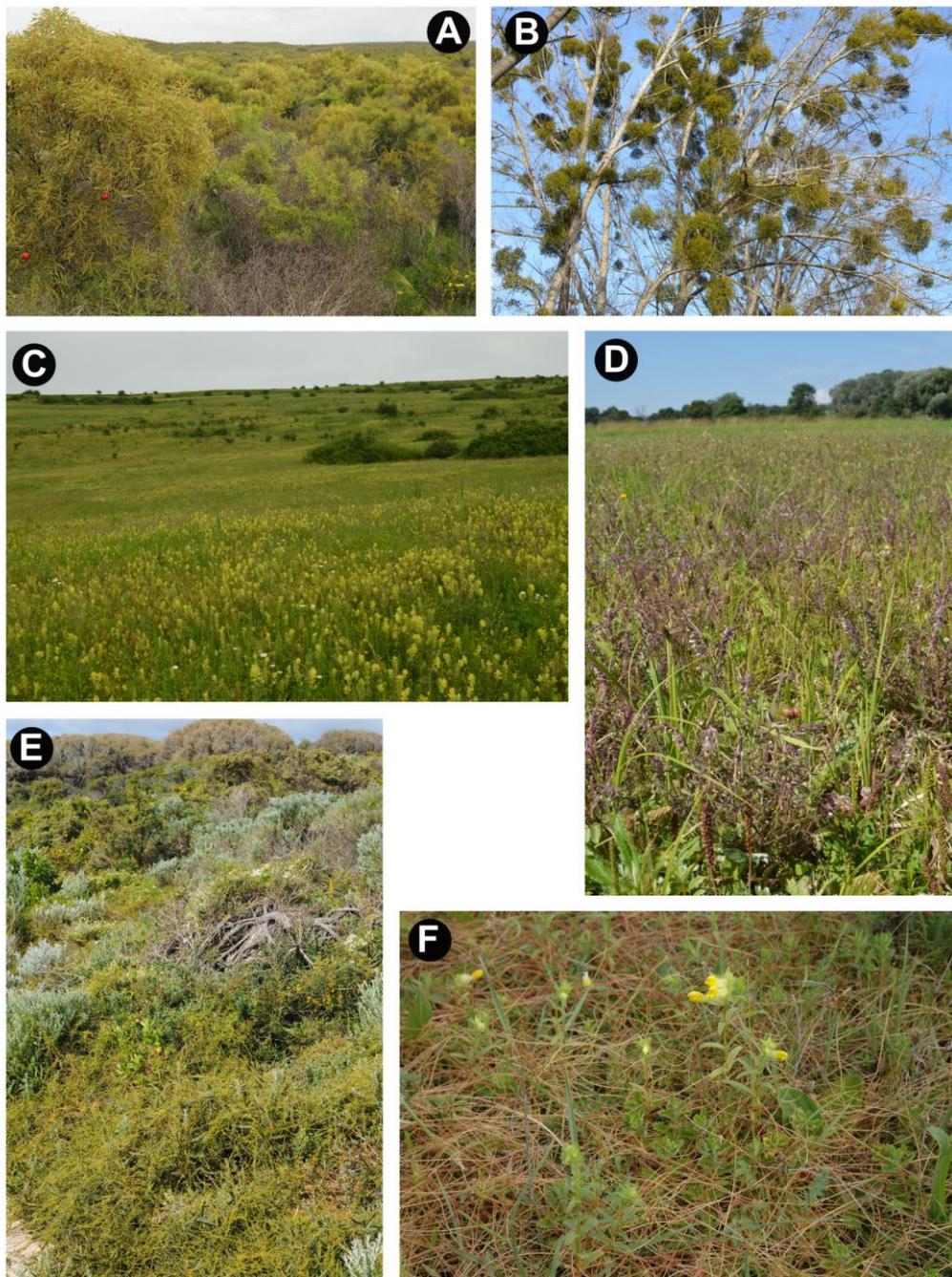
Fig. 2. Parasitic plants as vegetation dominants. A: *Santalum acuminatum* shrubs in Western Australian bush; B: *Viscum album* mistletoes parasitizing *Populus nigra* in floodplain forests, South Moravia; C: *Rhinanthus major* dominating a mesic meadow in Transsilvania; D: *Odontites vernus* dominance in a floodplain meadow in the regrowth stand after summer cut; E: *Cassytha* sp. in Western Australian bush; F: *Cuscuta* sp. (presumably *C. epithymum*) forming a dominance patch on a lowland meadow in Austrian part of Pannonia, note hyperparasitism on *Rhinanthus major*.

species may attain dominance in the communities (Fig. 2E) and recently have even been demonstrated to strongly suppress growth of leguminous invasive species (Prider *et al.*, 2009; Shen *et al.*, 2010). The parasitic-plant strategies which seem successful are thus rather diverse. Their success may be related to the history of global ecosystem and biota, i.e. the host environment. For instance, the evolution and radiation of Orobanchaceae coincides with the expansion of the grassland biome in the late Tertiary (Strömberg, 2011; Naumann *et al.*, 2013). The evolution and diversification of mistletoe life forms followed expansion of angiosperm-dominated forests in the late Cretaceous (Wang *et al.*, 2009). Loranthaceae mistletoes originated and radiated in the Oligocene following the expansion of savanna, their primary habitat at present (Vidal-Russell & Nickrent, 2008). The evolutionary success of *Cuscuta* may lay in the fact that most of the species of this genus are able to parasitize a wide range of hosts (Baráth & Csiky, 2012), which is otherwise rare among phloem-feeding parasites. This could possibly have been facilitated by the *Cuscuta* vine life form allowing interactions with many potential host species simultaneously (Fig. 2F) with possible repeated trials to attack also those hosts which were originally incompatible. Such situation may have triggered the evolution of a generalist phloem-feeding parasite. In summary, many different parasitic strategies underlie the success of individual parasitic plants. The lack of a universal hypothesis explaining the evolutionary pattern should not prevent us from acknowledging the evolutionary success and ecological roles of these successful groups of parasitic plants as well as extraordinary morphological and functional variability recognized in the whole functional group of parasitic plants.

2. Ecology of root-hemiparasitic plants

2.1. Introduction to root hemiparasites

Root-hemiparasitic plants are green photosynthetic plants which attack roots of other plants to withdraw resources of their xylem (Section 1; Irving & Cameron, 2009; Těšitel, 2016). To uptake the host resources they use a specialized organ, the haustorium which, in their case, is a modified root. Root hemiparasites comprise *ca* 2400 species (more than 50% of all parasitic plants, *ca* 0.5% of angiosperms) of three independent evolutionary lineages: Santalales, Orobanchaceae and Krameriaceae. Of these, the first two contain most of the diversity while Krameriaceae consist of a single genus with 18 species.

Extensive morphological diversity exists in root-hemiparasites ranging from tiny annual *Euphrasia* species occurring in alpine grasslands to large tropical forest trees with *Okoubaka aubrevillei* of Santalales, their largest representative, reaching up to 40 m high (Veenendaal *et al.*, 1996). Root hemiparasites are a functional group distributed globally on all continents except the Antarctic and occurring in all major terrestrial habitats (Heide-Jørgensen, 2008). Most species however occur in open habitats such as temperate grasslands, alpine vegetation and (semi)arid vegetation (Těšitel, 2016).

Root hemiparasites have been demonstrated to substantially affect structure of plant communities and ecosystem processes (Press, 1998; Press & Phoenix, 2005; Watson, 2009) together with other parasitic plant groups, the mistletoes (Watson, 2001) and parasitic vines (Callaway & Pennings, 1996). Some species (e.g. *Rhinanthus* spp.) are recognized for their ecosystem engineering capacity which may increase community diversity (Pywell *et al.*, 2004; Těšitel *et al.*, 2017) while others (e.g. *Striga* spp.) are recognized as serious weeds threatening the production of agriculture (Pennisi, 2010; Parker, 2013).

In this text, I first aim to introduce the physiological and ecological mechanisms of the root-hemiparasitic interaction. Second, I explain how these fundamentals underlie community and ecosystem effects recognized in a series of root-hemiparasitic species. And third, I discuss ecological applications of root-hemparasitic plants, which are based on their effects on plant communities and ecosystems. I also outline possible future research directions and applications of root-hemiparasitic plants in ecological restorations and agriculture.

2.2. Ecophysiological mechanisms of the hemiparasite-host interaction

The life cycle of a hemiparasite starts by seed germination as in other plants. The germination may be spontaneous in favourable conditions or may require an external stimulus to break seed dormancy. In most species, the dormancy-breaking factor is environmental; germination is triggered by a period of low temperature (Curtis & Cantlon, 1968; ter Borg, 2005; Liebst & Schneller, 2008), which in temperate species secures that the seedlings appear in spring when the conditions are favorable for seedling survival. Following germination, the seedling grows independently of a host. It produces a root system to forage for host roots and uptake water and mineral nutrients from the soil. The formation of haustoria and establishment of host connection usually follows after a period lasting few days to few weeks and is facilitated by chemical clues (haustorial inducing factors) which are excreted from host roots (Yoshida *et al.*, 2016). The unattached seedlings of most hemiparasites display inefficient physiology with low rates of photosynthesis and frequently observed imbalance of mineral nutrient concentration. This results in in poor growth or even premature death if host attachment is not established (Mann & Musselman, 1981; Seel *et al.*, 1993; Fer *et al.*, 1994; Lechowski, 1996; Matthies, 1997; Jiang *et al.*, 2007). While, there are some exceptions of hemiparasites that are able to grow decently without a host, such as *Odontites vernus, Euphrasia minima* (Matthies, 1998) or *Santalum acuminatum* (Radomiljac *et al.*, 1999), there is no empirical evidence reporting unattached hemiparasites from natural conditions. Some root hemiparasites evolved an advanced strategy of host-contact establishment. These species require a chemical trigger from the host to initiate germination (Section 1, Fig. 1). The chemical signals used to trigger germination are called strigolactones (Cardoso *et al.*, 2011; Yoshida *et al.*, 2016) and were identified to play a crucial role in plant communication with arbuscular mycorhizal fungi (Akiyama *et al.*, 2005) and later became recognized as a previously unknown type of plant hormones (Gomez-Roldan *et al.*, 2008). Typically, these species also have a fully heterotrophic seedling. This means that they practically avoid the stage of unattached seedling which a critical phase of the life cycle when most of the mortality occurs caused either by adverse environmental conditions or competitive pressure from the host community (Ameloot *et al.*, 2006; Ducarme & Wesselingh, 2009; Těšitel *et al.*, 2011).

Root hemiparasites withdraw resources from xylem vessels in the host roots. This nature of the anatomical connection determines resources taken up from the host, i.e. water, mineral nutrients, but only a limited amount of organic carbon. The unidirectional flow of resources from the host to parasite is underlain by high concentration of sugar alcohols, which are

osmotically active and lower the water potential of the hemiparasites (Hodgson, 1973; Press, 1995; Pageau *et al.*, 1998; Jiang *et al.*, 2005). Moreover, the resource flow may be further facilitated by some types of the xylem-xylem contact in the haustoria. In many hemiparasitic species (typically those of Santalales and Krameriaceae but also some Orobanchaceae) either cell wall or parenchyma cells are present on the host-parasite interface (Tennakoon *et al.*, 1997; Tennakoon & Cameron, 2006; Brokamp *et al.*, 2012). While water and some smaller molecules can pass through cell walls, the parenchyma cells may actively transport nutrients from host to the parasite facilitating uptake of greater molecules. A number of root-hemiparasitic species have however evolved open xylem continuity in the haustoria (Hibberd & Jeschke, 2001). Such continuity allows mass flow of xylem sap from the host to the parasite and is typical of species of Orobanchaceae genera *Striga* (Dörr, 1997) and *Rhinanthus* (Cameron *et al.*, 2006). These hemiparasites typically have highly elevated transpiration rates which greatly facilitates resource uptake from the hosts. Moreover, Orobanchaceae of the Rhinanthoid clade possess specialized hydathode-trichomes on their leaves which excrete water during night-time when transpiration does not proceed (Govier *et al.*, 1968; Světlíková *et al.*, 2015).

All water and mineral nutrition of root hemiparasites is typically of the host origin and may account for a substantial proportion of these resources taken up by the host (Ehleringer & Marshall, 1995; Jiang *et al.*, 2003, 2004). By contrast, carbon nutrition used to be hypothesized to be dependent solely or mostly on hemiparasites' photosynthesis. This was based on their morphology which in most cases resembles that of non-parasitic plants and in recent decades also on gas-exchange measurements indicating rates of photosynthesis comparable to those found in other plants (Fer *et al.*, 1994; Seel & Press, 1994; Lechowski, 1996; Těšitel *et al.*, 2011). Earlier reports on insufficiency of hemiparasites photosynthesis to secure carbon nutrition in a series of temperate hemiparasitic Orobanchaceae (Press *et al.*, 1988; Press, 1989) can nowadays be quite safely considered mistakes attributable to limitations of gas-exchange measurement instrumentation available at that time. Exceptions of this are however species of the genus *Striga*, photosynthesis of which was demonstrated to be generally low (Graves *et al.*, 1992; Cechin & Press, 1994). Similarly, species of genera *Tozzia* and *Rhynchocorys*, which are holoparasitic in the initial phase of their life (Section 1) may, be presumed to display reduced photosynthetic ability; however no empirical data are available in this respect.

Still, many root hemiparasites obtain organic carbon from their hosts despite the efficiency of photosynthesis and the exclusive connection to host xylem. This is because xylem sap of the hosts contains certain concentration of carbon (usually around 5-10 mmol org. C/l),

mainly in the form of amino-acids or organic acids (Govier *et al.*, 1967; Seel & Jeschke, 1999; Alvarez *et al.*, 2008). The transfer of organic compounds from host to hemiparasite was first demonstrated by a ^{14}C-radioisotope labelling study of the model hemiparasitic associations of *Odontites vernus* with *Hordeum vulgare* and *Trifolium repens* hosts (Govier *et al.*, 1967). While this approach successfully identified numerous compounds translocated from the host to the parasite, it was largely qualitative and thus could not provide information on the quantitative contribution of host-derived carbon to the parasite carbon budget. The first quantitative assessment followed two decades later and was based on an analysis of carbon-stable isotopic composition of biomass of two *Striga* species attached to hosts with C_4 photosynthetic pathway (Press *et al.*, 1987). C_4 plants are known to differ in carbon stable-isotopic composition of assimilates from C_3 plants (Boecklen *et al.*, 2011). All hemiparasites use the C_3 pathway while a number of hosts are C_4 plants. Comparisons between the actual stable-isotopic composition of a hemiparasite attached to a C_4 host with that of hemiparasite attached to a C_3 host or a prediction based on gas-exchange measurement can thus be used to estimate proportion of host-derived carbon in hemiparasite biomass. The latter approach was used by Press et al. (1987), which resulted in an estimate of 28% and 35% of host-derived carbon in hemiparasite biomass in *S. hermonthica* and *S. asiatica*, respectively. Comparable proportions of heterotrophic carbon in hemiparasite biomass were identified also in a number other root-hemiparasitic species including temperate species of genera *Euphrasia* and *Rhinanthus* (Těšitel *et al.*, 2010a). Recent research has however identified extensive variability of heterotrophic carbon proportion present even within a single host-hemiprasite association. The host contribution to carbon budget was demonstrated to vary during ontogeny and also differ between below- and above- ground parts of the hemiparasite (Pageau *et al.*, 1998; Santos-Izquierdo *et al.*, 2008). Increased proportions of host-derived carbon were found in hemiparasites which were shaded, i.e. their photo-assimilation was limited by an external factor (Těšitel *et al.*, 2011). Most recently, a glasshouse experiment with *Rhinanthus alectorolophus* (Těšitel *et al.*, 2015b) has demonstrated that contributions of heterotrophic and autotrophic pathways to the carbon budget of hemiparasites largely depend on the availability of other resources and physiological balance between the host and parasite. Highest proportion of host-derived carbon was found in hemiparasites that were stressed by simultaneous low availability of water and mineral nutrients, which had a strong negative impact on their photosynthetic ability. Hemiparasite biomass also contained elevated proportions of host derived carbon when the balance of the hemiparasitic assotiation was shifted towards the hosts' side due to the simultaneous abundance of both abiotic resources,. This indicates that host-derived carbon is used as a back-up resource when hemiparasite's own

photoassimilation is limited. It is also notable that the amount of carbon transferred from the host to the hemiparasite accounted for approximately 5% of total carbon in host above ground biomass (Těšitel *et al.*, 2015b) irrespective of experimental treatment. This indicates that carbon loss is not responsible for a major part of harm inflicted to the host by hemiparasitism.

2.3. Ecology of the hemiparasite-host interaction

The hemiparasitic interaction between a root hemiparasite and its host has an ambiguous nature. It is a clear case of parasitism below ground, where the parasite benefits from resources taken up from the host. Hemiparasites are mostly strong parasites which generally cover their needs for abiotic resources by parasitism. They also benefit from the fact that they do not need to invest into extensive root systems. Above-ground, however, a host and a hemiparasite are just two green plants that compete for light (Matthies, 1995; Fibich *et al.*, 2010), an interaction which is further strengthened by the spatial proximity of their shoots (Keith *et al.*, 2004). Root hemiparasites are mostly considered or assumed poor competitors (Hellström *et al.*, 2004; Cameron *et al.*, 2009; Fibich *et al.*, 2010; Borowicz & Armstrong, 2012). The effect of competition for light suppresses hemiparasite growth (Matthies, 1995; Těšitel *et al.*, 2011; Mardoian & Borowicz, 2016) but also increases seedling mortality (Těšitel *et al.*, 2011; Mardoian & Borowicz, 2016). The latter should have even stronger consequences for the population dynamics in particular considering the annual life history typical of many root-hemiparasitic species especially in Orobanchaceae (Tank & Olmstead, 2008; Těšitel *et al.*, 2010b). Elevated competitive pressure from the host (community) can largely be expected in ecosystems with favorable climate and with abundant below-ground resources (water and mineral nutrients), i.e. sites with high above-ground primary productivity (Hautier *et al.*, 2009). Hemiparasite populations have repeatedly been demonstrated to decrease in density at sites of elevated productivity; however the individuals having survived the critical seedling stage produced more biomass and/or more seeds (van Hulst *et al.*, 1987; Mudrák & Lepš, 2010; Těšitel *et al.*, 2013). It is likely that the surviving individuals were exceptionally well attached to their hosts (Keith *et al.*, 2004); their survival may hence be facilitated by heterotrophic carbon acquisition (Těšitel *et al.*, 2011). The elevated growth can then be attributed to elevated soil resources on which the hemiparasites response by an increase of photosynthesis similarly to non-parasitic plants (Simier *et al.*, 2006; Těšitel *et al.*, 2015b) and subsequent elevated individual fitness (Mudrák & Lepš, 2010; Hejcman *et al.* 2011; Těšitel *et al.* 2013). Still, the population may become exterminated since the elevated fecundity of the hemiparasites does not compensate for the decrease of population density under productivity level above certain

threshold. For instance, *Rhinanthus minor* population persistence was largely dependent on import of seeds from the surrounding in a field fertilizer experimental setup if productivity of the meadow was higher than 5t dry mass per hectare (Hejcman *et al.*, 2011).

Both parasitic and competitive components of the root-hemiprasitic interaction were included in a model of hemiparasite population dynamics (Fibich *et al.*, 2010). This model identified equilibria of stable coexistence between a parasite and a host under low to moderate productivity. By contrast, parasite population was predicted to perish under very low and high productivity values, caused by insufficient host resources and competitive pressure from the host, respectively. Such model is largely in line with empirical evidence from field experiments described in the previous paragraph. However, there are two effects that may counter-act the effect of competition on root-hemiparasites. First, parasitism may contribute significant amount of heterotrophic carbon, which may support parasite vertical growth and facilitate escape from competition (Těšitel *et al.*, 2011). Some species with holoparasitic-seedling stage (*Tozzia alpina*, *Rhynchocorys elephas*, *Striga asiatica*) were even observed to be able to flower and reproduce under heavy light deficiency (Fig. 3A,B; Dörr, 1997). Second, infection by a root hemiparasite may inflict substantial harm to the host which may decrease its competitive ability. The suppression of host growth by hemiparasitism mostly impacts shoots more than roots (Těšitel *et al.*, 2015b; Matthies, 2017), which makes this effect a crucial determinant of above-ground competition. Hemiparasitism was recently suggested to have a disproportionally great impact on clonal hosts (Demey *et al.*, 2015; Mudrák *et al.*, 2016), which are typically strong competitors in temperate grasslands (Gough *et al.* 2012; Herben *et al.*, 2014). This strategy may strongly decrease the intensity of above-ground competition and create gaps for seed regeneration, which may facilitate persistence of hemiparasite populations (Lepš & Těšitel, 2015). An extreme case of hemiparasite causing harm to its hosts to decrease competitive pressure was reported for *Okoubaka aubrevillei*. This species of Santalales is a tree growing in tropical rainforests, a habitat characteristic by extreme intensity of competition for light (Grace & Tilman, 1990). To facilitate regeneration from seeds, *O. aubrevillei* saplings inflict extreme harm to its hosts, some of which may even be killed (Veenendaal *et al.*, 1996). Disproportionally greater negative effects are exerted upon fast-growing hosts, which has clear benefit for the parasite in terms of avoiding competition. The population dynamics model of Fibich *et al.* (2010) thus needs further generalization to account for these cases which apparently contradict its prediction.
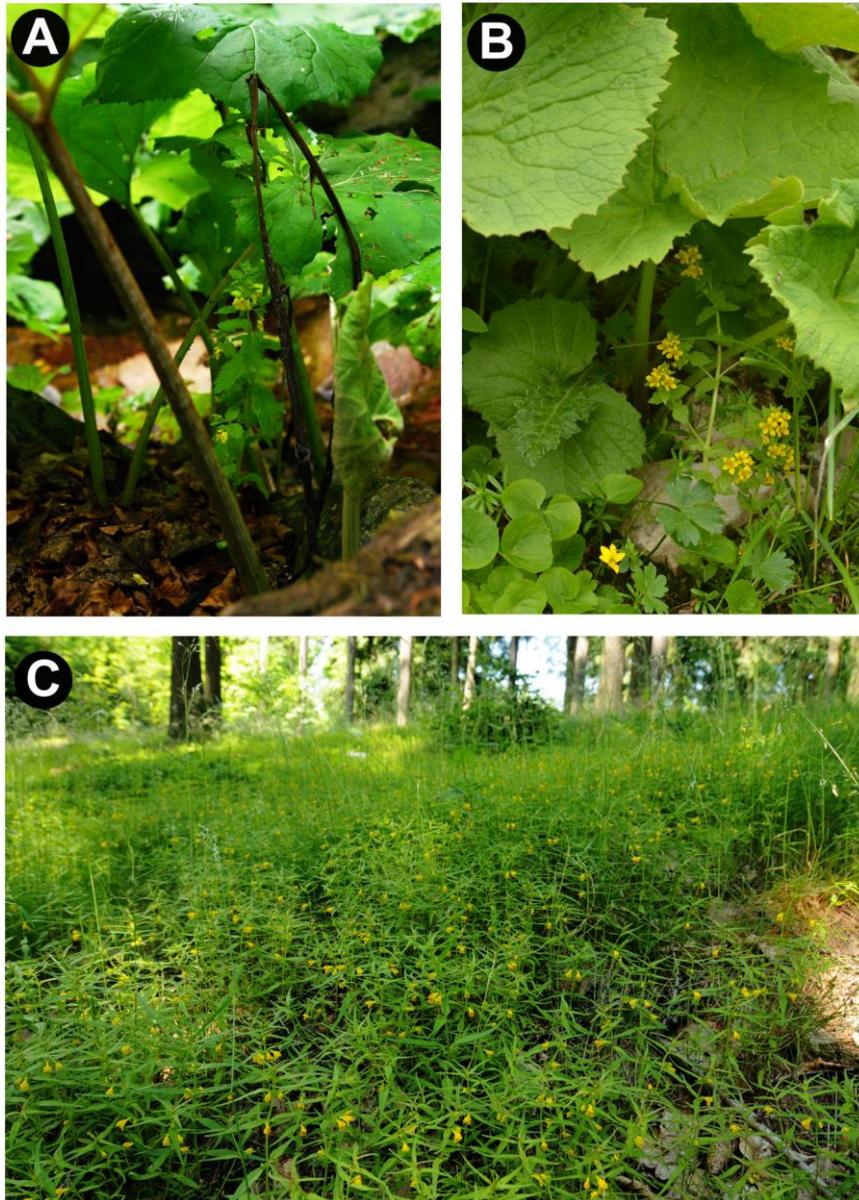
Fig. 3. Hemiparasitic strategy in environment of heavy light deficiency. A,B: *Rhynchocorys elephas* and *Tozzia alpina* growing under the canopy of *Petasistes* spp.; both species have long-lasting underground heterotrophic stage. Shoots are only produced for the purpose of generative reproduction. C: Dense stand of *Melampyrum sylvaticum* in a shady spruce-forest understory.

Root hemiparasites are mostly recognized as generalist parasites though the host range may be narrower in those species requiring host induction for germination, e.g. the *Striga* species (Parker, 2013). However, individual hosts markedly differ in their quality, i.e. how much they support hemiparasite growth. Some species may be even resistant to hemiparasitic infection. This may be based either on pre-attachment mechanism related to chemical signaling before the haustorial initiation or on post-attachment mechanisms when the host blocks resource

transfer from its vascular bundles (Cameron *et al.*, 2006; Yoder & Scholes, 2010). The post-attachment resistance mechanism may be recognized by inspection of haustorial anatomy as was exemplified on the interaction between *Rhinanthus minor* and *Plantago lanceolata* resistant to *Rhinanthus* infection (Cameron *et al.*, 2006; Rümer *et al.*, 2007). Interestingly, *P. lanceolata* had earlier been demonstrated as a very good host of several hemiparasitic *Euphrasia* species (Yeo, 1964). This indicates that the root-hemiparasitic interaction depends on species identity of the host and the hemiparasite and there are no universal good or bad hosts. Nitrogen-fixing legumes and grasses have been repeatedly suggested as better hosts than 'forbs' at least for a majority of hemiparasitic Orobanchaceae, which was also supported by certain empirical evidence (Seel & Press, 1993, 1994; Svensson *et al.*, 2001; Cameron *et al.*, 2006). However, recent studies investigating multiple host associations of *Rhinanthus minor* (Rowntree *et al.*, 2014) and *Melampyrum arvense* (Schädler *et al.*, 2005; Matthies, 2017) did not support such hypothesis. Similarly, host quality of hemiparasitic Santalales is not determined by any simple difference between functional groups. Instead, there seems to be a continuous pattern high quality hosts to hosts of very poor quality (Radomiljac *et al.*, 1999; Calladine *et al.*, 2000; Guo & Luo, 2010), presence of which may even suppress hemiparasite growth compared to unattached individuals (Radomiljac *et al.*, 1999). Below the species level, an interplay between host and hemiparasite genotypes was identified to significantly affect the outcome of the interaction (Rowntree *et al.*, 2011). Similarly, genotypes resistant to hemiparasitic infection are known from many field crops attacked by *Striga* species (Yoder & Scholes, 2010), which highlights the importance of genetic variability for hemiparasitism.

Field trials generally identified a large number of species to which root-hemiparasitic plants attach. In addition, certain selectivity for some taxonomic groups (and avoidance of others) is also frequently observed. For instance, Suetsugu *et al.* (2008) reported *Thesium chinense* attached to 22 species of 11 families with grasses to be positively selected while the haustoria formed on legumes were of larger size. By contrast, Dostálek & Münzbergová (2010) reported frequency of *Thesium linophyllon* attachments to host species largely proportional their root abundance. Gibson & Watkinson (1989) reported a number of significantly avoided hosts of *Rhinanthus minor* while a few were selected positively. Interestingly, *Plantago lanceolata*, known to be a resistant host (Cameron *et al.*, 2006), was shown to be positively selected in this study (though the haustoria can be assumed to be non-functional). Most recently, (Holá *et al.*, 2017) used a DNA-barcoding approach to identify host associations of three root-hemiparasitic Orobanchaceae (*Rhinanthus minor, R. major* and *Melampyrum nemorosum*),

which co-occurred at one site. The three species notably differed in selectivity for hosts at the family taxonomic level. Interestingly, many haustorial connections were identified between hemiparasitic species themselves both between and within species. Detailed field surveys are however rare due to methodological difficulties of associated with root-system inspection. In this respect, the DNA-barcoding approach may facilitate the workflow though there is still a lot of space for improvement and refinement of this method (Holá *et al.*, 2017). Deficiency of direct data on host identity is a critical issue of almost all studies aiming at community ecology of root hemiparasites. There are only few studies where above ground patterns of vegetation or results of manipulative experiments are compared with parasitic associations below-ground. An example of such a study is represented by a removal experiment with *Pedicularis kansuensis* in which positively selected hosts, grasses and legumes, significantly increased after weeding of the hemiparasite (Bao *et al.*, 2015).

The hosts' side of the interaction is characterized by harm inflicted by hemiparasitism, which is mostly measured as a reduction of its biomass production (or crop reduction in the case of hosts important for agriculture). The negative effects of hemiparasites on the hosts are very variable, ranging from negligible to lethal. Besides the extreme host damage inflicted by *Okoubaka aubrevillei* described above, hemiparasitic species with open xylem contacts in their haustoria, such as *Striga* or *Rhinanthus*, tend also to be highly host-damaging (Parker, 2013; Těšitel *et al.*, 2015b). Multiple physiological mechanisms are involved in the harmful effect of the hemiparasites on their hosts. Loss of abiotic resources is certainly the principal factor in most cases while loss of organic carbon seems of minor importance (Těšitel *et al.*, 2015b). Recent experiment with manipulated availability of water and mineral nutrients identified strong interactive effects of these two resources on harm inflicted to maize and wheat hosts of *Rhinanthus alectorolophus* (Těšitel *et al.*, 2015b). This indicates that loss of either resource due to parasitism may underlie the host damage. In this experiment, the largest harm was inflicted when either of the resources was provided in abundance while the other was deficient. Even damage to host photosynthesis (maximum quantum yield) was identified under dry and nutrient rich conditions. Simultaneous abundance of both resources largely alleviated the effect of parasitism on the host, while simultaneous deficiency was stressful for the parasites which consequently limited the harmful effect on the hosts (Těšitel *et al.*, 2015b). While individual hemiparasitic species differ in their intrinsic harmfulness the damage inflicted to the hosts depends also on host species. Obviously, resistant hosts are harmed less than susceptible ones (Cameron *et al.*, 2006). Several studies actually reported a tight correlation between host quality

and damage inflicted by hemiparasitism (Matthies, 1996; Marvier, 1998). However, a recent extensive study with *Melampyrum arvense* (Matthies, 2017) testing 27 different hosts identified a group of hosts which supported vigorous growth of the hemiparasites but suffered relatively little harm. The growth of two legumes, *Trifolium pratense* and *Lotus corniculatus*, was actually negligibly reduced while supporting a decent growth of the parasite. Such pattern was also reported for some legume hosts also in studies with *Rhinanthus* spp. (Davies *et al.*, 1997; Joshi *et al.*, 2000; Cameron *et al.*, 2006). These results are mostly based on simple cultivation trials comparing host performance between infected and uninfected individuals. Largely ignored in such experimental setups, the litter input from hemiparasitic plants may however positively affect productivity of host community (see the next section for details). A recent study has found that high quality hosts of a hemiparasite may obtain disproportional benefit, which may partly compensate for the negative effect of parasitism (Fisher *et al.*, 2013). In real communities, competitive interactions between host and non-host plants and with other trophic levels are also involved together with the effect of the environment, all of which may have strong modifying effects on hemiparasitic interactions.

2.4. Community and ecosystem ecology of parasitic plants

Root-hemiaprasitic plants are a generally omnipresent component of terrestrial vegetation, in particular open (i.e. non-forest) plant communities (Heide-Jørgensen, 2008; Těšitel *et al.* 2015a). Due to their unique ecophysiology, trophic status and interactions with the hosts they have been recognized for their ability to influence structure of plant communities (Phoenix & Press, 2004). The community and ecosystem effects of some root-hemiparasitic species are so pronounced that they are even considered keystone species or ecosystem engineers (Phoenix & Press, 2004; Cameron *et al.*, 2005; Press & Phoenix, 2005; Watson, 2009; Decleer *et al.*, 2013; Těšitel *et al.*, 2017).

Root-hemiparasites may be expected to occur mostly in low-productiveand nutrient poor environments. Under such conditions, they would benefit most from the parasitism, providing low cost access to mineral nutrients (Phoenix & Press, 2004, 2005; Fibich *et al.*, 2010; Borowicz & Armstrong, 2012). In addition, corresponding plant communities tend to be of relatively low sward or stem density which implies good light availability. As a result, the effects of above-ground competition, a crucial factor limiting occurrence of root-hemiparasites (see section 2.3), are rather low. Most Krameriaceae and many of root-hemiparasitic Santalales largely conform to this scheme occurring in low-productive (semi-)arid habitats (Giannini *et al.*, 2011; Heide-Jørgensen, 2013). Still, a number of Santalales are tropical-rainforest trees

detailed ecology of which has yet to be described. In temperate regions, a recent analysis of ecological niches of root-hemiparasites in the Czech Republic (Central Europe) identified a relatively wide range of habitats suitable for at least some root-hemiparasitic species (Těšitel *et al.*, 2015a). While some species were indeed found to occur at sites of low-productivity limited by nutrient availability, water deficiency, short vegetation season or a combination of these (e.g. *Euphrasia stricta*, *Thesium linophyllon*m, *Odontites luteus*, *Pedicularis sylvatica*, *Rhinanthus riphaeus*), some others grow at sites with relatively high productivity. *Euphrasia officinalis Melampyrum arvense, M. pratense, Rhinanthus alectorolophus, R. major, R. minor* can be found over most of the range of the soil fertility gradient but only if such sites are relatively dry as indicated by Ellenberg indicator values. Some of these species may also be found on moist sites but their niche is restricted to oligotrophic places at this end of moisture gradient. Such pattern corresponds well to the experimental study manipulating water and mineral nutrients, which demonstrated loss of advantage of parasitism and alleviation of its effect on the host when both resources were provided in abundance (Těšitel *et al.*, 2015b). Two root-hemiparasitic species, *Odontites vernus* and *Pedicularis palustris*, may however grow even in these conditions, which is underlain either by disturbance, which limits competition and creates regeneration gaps in the sward or by the selectivity of the hemiparasite for dominant competitors which are extremely harmed by parasitism (Decleer *et al.*, 2013), respectively. Three species of *Melampyrum* (*M. nemorosum*, *M. pratense*, *M. sylvaticum*) grow in understory of closed-canopy forests (Fig. 3C), where they are also unique by their annual life history (Těšitel *et al.*, 2015a). A recent model of *M. pratense* carbon budget based on gas-exchange data and light-condition monitoring throughout the growth season however suggests insufficiency of their autotrophic carbon assimilation pathway (Světlíková et al. *unpublished*). In particular, the predicted carbon balance was close to zero in summer, when energy- and carbon-demanding seed production is in progress. This points to possible importance of heterotrophic carbon acquisition in these species, which is however difficult to demonstrate directly.

Presence of root-hemiparasites usually results in possibly strong negative effects on host community productivity (Davies *et al.*, 1997; Joshi *et al.*, 2000; Ameloot *et al.*, 2005; Bardgett *et al.*, 2006; Stein *et al.*, 2009; Mudrák & Lepš, 2010; Borowicz & Armstrong, 2012; Demey *et al.*, 2013a; Bao *et al.*, 2015)., which is underlain by suppression of host growth (Phoenix & Press, 2004; Press & Phoenix, 2005). Moreover, in many cases, a decrease of total productivity (i.e. host + hemiparasite biomass) was observed (Davies *et al.*, 1997; Ameloot *et al.*, 2005;

Stein *et al.*, 2009; Mudrák & Lepš, 2010; Demey *et al.*, 2013a; Bao *et al.*, 2015), which means that parasite biomass did not compensate for the loss on the hosts' side. This effect is usually attributed to lower photosynthetic resource-use efficiency in hemiparasites (Seel & Press, 1994; Westbury, 2004). However, this effect on total community productivity is far from universal. In some cases, higher community productivity was observed, e.g. in case of species-poor assemblages in a biodiversity experiment (Joshi *et al.*, 2000). In an observation-based study, hemiparasitic *Castilleja occidentalis* was found to be associated with high-productivity patches in alpine tundra (Spasojevic & Suding, 2011). The positive influence of root-hemiparasites may largely be attributed to the effect of their litter on the community. Due to their ability to withdraw mineral nutrients from the hosts and relatively low photosynthetic resource-use efficiency (Seel & Press, 1994; Press & Phoenix, 2005), litter of hemiparasites displays high mineral nutrient concentration, often higher than that of co-occurring species (Quested *et al.*, 2002, 2003a,b, 2005). This implies higher rates of litter decomposition and consequent release of nutrients (Quested *et al.*, 2003b; Demey *et al.*, 2013b). The nutrients are also frequently released from litter during the growth season, when the demand for them is high (Quested *et al.*, 2005; Demey *et al.*, 2013b). These positive effects of the litter pathway on community productivity may at least partly compensate for the negative effect of parasitism. Recent experiments have moreover demonstrated that the largest benefits from the litter pathway are acquired by host plants species (Fisher *et al.*, 2013) or plants with fast-growth strategy (Demey *et al.*, 2013b), which may either compensate for the losses to parasitism or even further increase biomass production, respectively. In addition, hemiparasites have been demonstrated to increase average nutrient concentration in biomass (Ameloot *et al.*, 2008; Fisher *et al.*, 2013), which may have additional impacts on nutrient cycling. It is notable that many accounts on reduction of productivity by hemiparasites are based on peak biomass production in early to mid-summer. In annual hemiparasites, such as *Rhinanthus* spp., this captures predominantly the effects of parasitism, while the effect of nutrient release from litter should affect the community predominantly in the second half of the season (late summer, autumn), which is usually not monitored.

Root hemiparasites do not influence only the productivity but exert complex direct and indirect effects on the community structure. Suppression of host species may result in altered competitive hierarchy in the communities (Gibson & Watkinson, 1991; Marvier, 1998; Mudrák & Lepš, 2010; Borowicz & Armstrong, 2012; Bao *et al.*, 2015; Demey *et al.*, 2015). If host species are competitive dominants and a large reduction of their growth is inflicted,

hemiparasites may open space for subordinate species and consequently increase community diversity (Davies *et al.*, 1997; Pywell *et al.*, 2004; Decleer *et al.*, 2013; Těšitel *et al.*, 2017). This is further supported by creation of gaps following annual hemiparasite die back in mid- to late summer, which may facilitate their and other species establishment (Joshi *et al.*, 2000; Lepš & Těšitel, 2015). However, if a subordinate species is parasitized or the suppressed dominant is replaced by another one, biodiversity may remain unchanged or may be even lower at plots with the parasites (Gibson & Watkinson, 1992; Mudrák & Lepš, 2010). Nonetheless, a recent analysis based on extensive vegetation plot database demonstrated that most root hemiparasites occur in significantly more species-rich vegetation than expected by chance and some of the hemiparasitic species are among the species most tightly associated with high community diversity (Fibich *et al.*, 2017). While this pattern is probably not caused solely by the positive effect of hemiparasites on diversity and other mechanisms are involved (namely the preference of hemiparasites to grow in low-competitive habitats which are frequently species rich), this results represent an upscale of the hemiparasite-diversity relationship from the local level of single site experiments. Taken together with their effect on productivity, it seems that hemiparasites may decrease productivity in rather productive environments via the parasitic pathway and harm inflicted to the fast-growing dominants, while in low productive environments, the positive effect of the litter pathway could prevail. Such hypothesis was introduced by Watson (2009) suggesting that root-hemiparasites create environment of intermediate productivity and open opportunities for generative reproduction, which is largely beneficial for them in terms of host resource availability and limited effect of above-ground competition. Eventually, communities of intermediate productivity are also those which display highest biodiversity worldwide (Fraser *et al.*, 2015).

The ecological interactions of root hemiparasites are not limited to the plant component of the ecosystems. Strong interactions with organisms of other trophic levels were observed and described in the literature. Root hemiparasites are mostly non-mycorrhizal. In recently described notable exceptions to this, two species of *Pedicularis* were demonstrated to have low-colonization level of arbuscular mycorrhiza in their roots, which may contribute up to few percent of their phosphorus nutrition while the rest is provided by the host (Li *et al.*, 2013). However, strong indirect interactions with arbuscular mycorrhiza were reported. In a glasshouse experiment, a strong benefit was observed for *Rhinanthus minor* if attached to a mycorrhizal host, which was also more suppressed by hemiparasitism (Davies & Graves, 1998). In another experiment, interactive effects of mycorrhizal fungi and parasitism on community

structure were observed, with the effect of parasitism only apparent in mycorrhiza-infected communities (Stein *et al.*, 2009). Apart from mycorrhiza, presence of hemiparasite was demonstrated to influence fungal-to-bacterial ratio in soil, a major pattern of soil microbial communities (Bardgett *et al.*, 2006). A complicated four-member interaction was described between *Rhinanthus major*, its grass host (*Festuca pratensis*), alkaloid-producing endophyte present in grass roots and an aphid herbivore (Lehtonen *et al.*, 2005). The hemiparasite took up alkaloids of the host, which are produced by the symbiotic endophyte and protect the host against herbivory if it is not parasitized. If parasitized, the hemiparasite benefited from the herbivory protection while the grass host did not. Thus, the hemiparasite changed the originally mutualistic interaction between the grass and the endophyte to parasitic. Alkaloids, but this time of intrinsic host origin, also played an important role in another complex interaction. Two *Castilleja* species were found to benefit from lupin hosts (*Lupinus albus, L. argenteus*) and an uptake of alkaloids from them due to improved pollination and reduced herbivory (Adler, 2000, 2002). Hemiparasites may also mediate herbivory of hosts plants. In a glasshouse experiment, *Rhinanthus major* was demonstrated to decrease herbivory of acyanogenic *Trifolium repens* hosts while no such effect was observed in the case of cyanogenic plants (Puustinen & Mutikainen, 2001). In a multi-host experiment. Palatability of *Melampyrum arvense* biomass was found to strongly differ if attached to different host species but unrelated to host species palatability, which indicates a complicated underlying mechanism based on the interaction of hemiparasitism and host anti-herbivory defense (Schädler *et al.*, 2005). Concerning root-hemiparasitic Santalales, vegetation containing shrubby hemiparasite *Exocarpos strictus* was demonstrated to host more species of birds and a higher abundance of arthropods compared to vegetation without the hemiparasite (Watson *et al.*, 2011).

To sum up, a number of root-hemiparasitic species were demonstrated to affect the community structure, productivity and diversity via either parasitic or facilitative interaction. These effects may reach beyond the plant community to the scale of the whole ecosystem. Some of them may also offer opportunities for ecological applications. More on that in the next section.

2.5. Applications of root hemiparasites in ecological restoration

The idea on application of root-hemiparasitic plants in ecological restoration and nature conservation stems from the experimental work of Davies *et al.* (1997) who demonstrated that presence of *Rhinanthus* species is associated with lower grassland productivity. This study comprised also an experiment manipulating *Rhinanthus* density by weeding, which

demonstrated suppression of grasses by the hemiparasites and reduction of sward density. Following this pioneering study, a number of further trials were done to test the applicability of *Rhinanthus* spp. (mostly *Rhinanthus minor*) in grassland restoration in Western Europe. The typical situations included either grassland sites which had been used for intensive agriculture and managed accordingly or former field used in agriculture. Either of these had been fertilized and the meadows also mown several times (>2) a year. Such high land-use intensity is known to greatly decrease diversity of the grassland ecosystem (Allan *et al.*, 2014, 2015; Lepš, 2014). Cease of fertilizer application combined with a decrease of mowing intensity may help restoring community diversity of meadows; however, this is largely impeded by high amount of residual soil nutrients and dominance of fast-growing clonal competitive grasses (Gough *et al.*, 2012; Lepš, 2014), which prevent establishment of other species. Similarly, in abandoned fields, competitive species may dominate after several years of succession even if the fields are seeded by dedicated seed mixtures of regional provenance (Prach *et al.*, 2014). Drastic measures such as topsoil removal or gramicide chemicals may be used to decrease dominant grass abundance and/or remove residual nutrients but these are costly and questionable from the environmental impact perspective. Therefore, the use of *Rhinanthus* sowing was tested as an alternative biological option. Application of *Rhinanthus minor* was demonstrated more beneficial to community diversity compared to the selective gramicide chemicals (Westbury & Dunnett, 2008) and supported establishment of significantly more target species sown at the beginning of the experiment. Another experiment identified a positive effect of supplementary soil surface scarification measure on establishment of *R. minor* on an abandoned field where a mixture of target grassland species was sown (Westbury *et al.*, 2006). In the same time, *Rhinanthus* itself was demonstrated to decrease grass dominance in the community and to increase community diversity. A similar experiment on a newly established meadow on ex-arable field demonstrated that *R. minor* can decrease grass dominance even at sites with high soil nitrogen concentration but only at high sowing density (1000 seeds $^{-2}$;Westbury & Dunnett, 2007). The most detailed experiment among these was conducted on a meadow of moderate productivity, which had been fertilized in the past and was dominated by a few grasses and forbs at the start of the experiment (Pywell *et al.*, 2007). The experimental treatments included sowing of *Rhinanthus minor* in different densities and sowing of a mixture of target species combined in a factorial design. *Rhinanthus* established at the plots where sown and later invaded also the unsown plots. A strong negative effect of *Rhinanthus* was found on sward height, which decreased by 50% at plots with a high hemiparasite density. By contrast, the effect on overall diversity as well as diversity of sown species was significantly positive. Analysis of species composition changes

identified a positive effect of *Rhinanthus* on a number of forb species, such as *Leucanthemum vulgare*, *Leontodon autumnalis*, *Plantago lanceolata, Prunella vulgaris*. The utility of *Rhinanthus minor* on grassland restoration was also tested in a multi-site experiment scaling up the findings of the other studies to the landscape scale (Hellström *et al.*, 2011). The success of these experiments with *Rhinanthus minor* resulted in its regular application in grassland restoration in Western European countries, in particular the UK (Blakesley & Buckley, 2016).

In addition to high land use intensity, grassland biodiversity is also threatened by abandonment, i.e. cessation of mowing. This process leads to a similar community structure with a few competitive dominants as in the case of high land-use intensity. However, species identity is usually different. Abandonment and associated expansion of dominants is a particular problem in species-rich meadow grasslands occurring in Central and Eastern Europe, some of which represent the most species-rich grassland from the global perspective (Wilson *et al.*, 2012; Dengler *et al.*, 2014; Chytrý *et al.*, 2015). Particular issue there is the expansion of *Calamagrostis epigejos*, a dominant clonal grass, which spreads not only to abandoned sites but also to vegetation managed by low-intensity mowing, i.e. the management type recommended to maintain biodiversity (Dengler *et al.*, 2014). The competitive strategy of this clonal species involves spread by rhizomes and resource storage in the roots, which make it robust against targeted measures applied above ground. However, a recent multi-site study (Těšitel *et al.*, 2017) demonstrated that the grass may be infected by hemiparasites of the genus *Rhinanthus*, namely *R. alectorolophus. R. alectorolophus* exerts a drastic effect on the grass and may even exclude it from the community within two years, in particular if its application is coupled with a moderate increase of mowing intensity. In addition, species diversity may be restored in a rather short term. Such effect was only identified at one site out of three; however this represented a typical case of abandoned intermittently wet meadow, which expands the potential of this finding. Based on these results and also other similar experiments waiting for publication, nature conservation in the Czech Republic has started to use the hemiparasites as a restoration measure at sites infested by *Calamagrostis epigejos*. Another example of a root hemiparasite suppressing a particular competitive dominant is a report of *Pediculartis palustris* which drastically reduced tall sedges (mainly *Carex acuta*) and transformed a tall-sedge vegetation into a fen meadow, a highly valuable community from the nature conservation perspective (Decleer *et al.*, 2013).

All these studies indicate a great potential of the use of root-hemiparasitic plants in ecological restoration and biodiversity conservation, which is further facilitated by detailed

application guidelines (Mudrák *et al.*, 2014; Těšitel, 2015; Blakesley & Buckley, 2016) However, there are always controversies connected with introduction of seeds of species on sites from which they were previously absent. Therefore, the hemiparasites should be used with caution. Preferably local seed sources should be used where possible. Ideal situation includes seeds transfers within a single site, which complies with the most strict requirements of nature conservation to preserve genetic resources and thus can be used even in nature reserves.

2.6. Future perspectives

The ecological interactions of root hemiparasites with their hosts are well understood particularly in grassland habitats and in the case of agricultural weeds. This knowledge is based on observations and experiments conducted *in situ*, which provides a good basis for understanding the ecology in the context of real communities and ecosystems as well as on glasshouse experiments which aim at identification of the nderlying physiological mechanisms. However, we still know very little about the ecology and ecophysiology of root hemiparasites growing in the forest vegetation. This includes e.g. *Melampyrum* species of Orobanchaceae and many woody species of Santalales. More information on their ecology, resource acquisition from the host and especially strategies of carbon acquisition in the shady environment may reveal new and possibly surprising ecological stories such as that of *Okoubaka aubrevillei* and its extreme effect on the hosts (see section 2.3).

The contemporary literature summarized here also contains a number of accounts on complicated ecological interactions where root hemiparasites play a central role. Most of these reports are however based on experiments in glasshouse conditions. The extent to which, these effects may be present in the context of real ecosystems remains questionable. Certainly some effects may be quite strong and frequent as demonstrated e.g. by field studies on stem-parasitic mistletoes which have a profound effects on nutrient cycling, productivity and community composition of several trophic levels (Watson, 2016). More studies aiming e.g. at direct and indirect interactions with mycorrhizal fungi, pollinators, invertebrate and vertebrate herbivores in the field conditions are thus needed to develop this topic.

One of the appealing question is the true nature of the interaction between root hemiparasites and Fabaceae. Both groups display specialized strategies of nutrient acquisition and Fabaceae frequently serve as hosts of the hemiparasites. While mostly high quality hosts, harm inflicted to them seems rather restricted at least in some species. A number of field experiments also did identify none or only moderately negative effect of hemiparasites on

legume abundance in the community. Therefore, they may be rather tolerant hosts. In such case, they may actually establish an alliance with the hemiparasites to suppress competitively superior grasses. Such hypothesis may be supported by existence of vegetation patches, where these groups co-occur in abundance (Fig. 4A) and both look rather vigorous while grasses seem strongly suppressed (Fig. 4B). Although such patches may be transient, repeated informal observations of the same site suggest that they persist for at least several years. If such community could be established on a large scale, there may be a number of applications in agri- and horticulture, such as designing low-intervention high-benefit grassland communities for orchard understory (Fig. 4C).
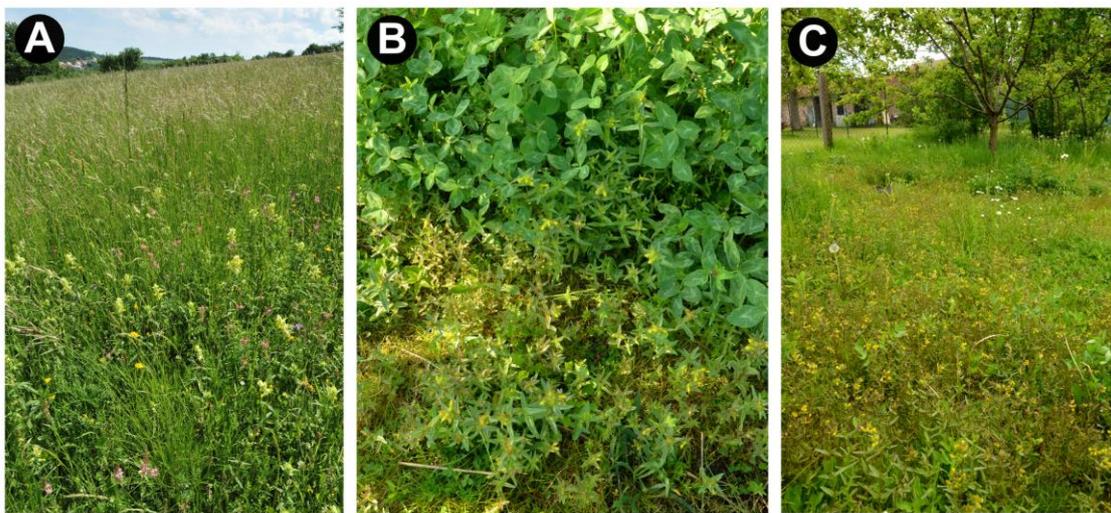
Fig. 4. Illustrations of possible alliances between root hemiparasites and legumes (A,B). A: Patch of *Rhinanthus alectorolophus* and *Onobrychys viciifolia* on a restored meadow near Suchov, Bílé Karpaty Mts.; B: Intraction of *Rhinanthus minor*, *Trifolium pratense* and the grass *Festuca rubra*. *Trifolium* seems to support vigorous growth of *Rhinanthus*, while *Festuca* looks strongly supressed. C: pilot application of the hemiparasites (*R. minor, R, minor*) in apricot orchard understory.

The role of hemiparasitic plants in ecological restoration and nature conservation is generally established due to recent strong development of the topic. However, practical experience indicates success at some sites, mixed effects at others and complete failure elsewhere. Scaling the research up to the large landscape scale is therefore needed to assess suitability of sites for hemiparasite application and identify underlying biotic and abiotic factors. This would greatly facilitate further use of hemiparasites by nature conservation and possibly also stakeholders.

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4. List of papers

1. **Těšitel J**. **2016**. Functional biology of parasitic plants: a review. *Plant Ecology and Evolution* **149**: 5–20.

2. **Těšitel J, Těšitelová T, Fisher JP, Lepš J, Cameron DD**. **2015**. Integrating ecology and physiology of root-hemiparasitic interaction: interactive effects of abiotic resources shape the interplay between parasitism and autotrophy. *New Phytologist* **205**: 350–360.

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6. **Fibich P, Lepš J, Chytrý M, Těšitel J**. **2017**. Root hemiparasitic plants are associated with high diversity in temperate grasslands. *Journal of Vegetation Science* **28**: 184–191.

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