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The bright side of parasitic plants: what are they good for?

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Abstract

Parasitic plants are mostly viewed as pests. This is caused by several species causing serious damage to agriculture and forestry. There is however much more to parasitic plants than presumed weeds. Many parasitic plans exert even positive effects on natural ecosystems and human society, which we review in this paper. Plant parasitism generally reduces the growth and fitness of the hosts. The network created by a parasitic plant attached to multiple host plant individuals may however trigger transferring systemic signals among these. Parasitic plants have repeatedly been documented to play the role of keystone species in the ecosystems. Harmful effects on community dominants, including invasive species, may facilitate species coexistence and thus increase biodiversity. Many parasitic plants enhance nutrient cycling and provide resources to other organisms like herbivores or pollinators, which contributes to facilitation cascades in the ecosystems. There is also a long tradition of human use of parasitic plants for medicinal and cultural purposes worldwide. Few species provide edible fruits. Several parasitic plants are even cultivated by agriculture/forestry for efficient harvesting of their products. Horticultural use of some parasitic plant species has also been considered. While providing multiple benefits, parasitic plants should always be used with care. In particular, parasitic plant species should not be cultivated outside their native geographical range to avoid the risk of their uncontrolled spread and the resulting damage to ecosystems.

Introduction

Most plants are photoautotrophic organisms, which need only fundamental abiotic resources for their essential vital processes. An exception to this is parasitic plants, which acquire resources by parasitizing other plants via a specialized organ called the haustorium. Developed as root or stem modifications, haustoria secure unidirectional connections between the vascular systems of host and parasite, enabling resource flow and freeing parasitic plants from many constraints to growth. While parasitism necessarily confers benefits to the parasites, it usually exerts moderate to strong negative effects on host growth and/or reproductive output. Several species of parasitic plants attack agricultural crops or

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- Parasitic plants may act as highways for transferring systemic signals among host plants.
- Harmful effects of parasitic plants on individual hosts suppress community dominants including invasive species, reduce competitive pressure, and may increase biodiversity.
- Parasitic plants enhance nutrient cycling and provide resources for other organisms thus contributing to facilitation cascades in ecosystems.
- Many parasitic plants are recorded to have medicinal values against a broad range of diseases.
- There is a long tradition of worldwide human use of parasitic plants, which have been cultivated for their products and aesthetic values.

trees used for production forestry. The most important of these are *Striga hermonthica* attacking cereals like sorghum (*Sorghum bicolor*), maize (*Zea mays*), and finger millet (*Pennisetum glaucum*; Parker, 2013), *Phelipanche ramosa* attacking a range of crops like tomato (*Solanum lycopersicon*), tobacco (*Nicotiana tabacum*), pea (*Pisum sativum*), lentil (*Lens culinaris*), carrot (*Daucus carota*), and sunflower (*Helianthus annuus*; Parker, 2013), and *Cuscuta campestris* infesting alfalfa (*Medicago sativa*), faba bean (Vicia faba), and sugar beet (*Beta vulgaris*; Parker, 2012). Forestry pests include e.g. *Arceuthobium* spp. attacking conifers in North America (Hawksworth and Wiens, 1996) and *Seymeria cassioides* damaging pine plantations (e.g. *Pinus clausa, Pinus elliottii, P. strobus*) in south-eastern USA (Musselman and Mann, 1978). These weedy species characterize the predominantly negative sentiment toward parasitic plants by the general public and agricultural sector (Pennisi, 2010), exacerbated by the general archetypal attitude toward parasites.

There is, however, much more to parasitic plants than presumed weeds. With *ca.* 4,500 species in total, parasitic plants represent a specialized yet heterogeneous functional group. Individual species differ in their trophic modes, associated functional traits, and phylogenetic origins (Westwood et al., 2010; Heide-Jørgensen, 2013; Těšitel, 2016). Parasitic plants are a ubiquitous component of terrestrial ecosystems worldwide, though their species richness and frequency varies between biomes and individual habitats (Heide-Jørgensen, 2008; Těšitel et al., 2015; Těšitel, 2016). Their ecological roles are also more complex than just negative effects on the host. Numerous parasitic plant species have been demonstrated to exert multifaceted ecological effects associated with altering competitive relations in the community and release of nutrient-rich litter facilitating nutrient cycling in ecosystems (Press and Phoenix, 2005; March and Watson, 2007; Watson, 2009; Demey et al., 2015; Watson, 2016; Těšitel et al., 2018). A number of species also provide resources for animals including food for herbivores, frugivores or pollinators, and shelter or nesting opportunities. These effects may trigger species composition change (Watson et al., 2011; Hartley et al., 2015) and, eventually, an increase of community diversity (Westbury et al., 2006; Watson and Herring, 2012; Fibich et al., 2017). Parasitic plants have also been used by humans for centuries either whole or as products originating from them. Interestingly, in the first systematic treatment of biology of parasitic plants, Job Kuijt (1969) included a section on “The uses of parasitic plants”, highlighting the many contributions of parasitic plants to human societies.

In this paper, we review the positive effects of parasitic plants and highlight recent advances on this topic. At the organismal level, we consider cases where parasitic plants positively influence host plants or nonhost organisms in terms of their growth, reproductive output or indirectly via modified ecological interactions. We also discuss positive effects on community structure and ecosystem processes. The second half of the paper is dedicated to the benefits to human society provided by parasitic plants. This includes ecosystem effects facilitating crop production and its sustainability, and direct use of parasitic plants as technical crops, food or medicinal resources. Finally, we discuss the use of parasitic plants in horticulture for aesthetic and cultural purposes.

Biology and ecology of positive effects of parasitic plants

Some aspects of parasitism may be positive even for the host

Parasitic plants typically exert negative effects on physiological processes and consequently the fitness of their hosts. However, several cases of positive effects on some host processes have been identified even within the intimate host–parasite interaction. In some root–holoparasitic associations, infected hosts may display higher rates of photosynthesis and nutrient uptake capacity compared to uninfected plants (Hibberd et al., 1998; Irving and Cameron, 2009). Such positive effect on photosynthesis is nevertheless not reflected by host growth although transient increase of host relative growth rate has also been documented (Dale and Press, 1998).

Many parasitic plants parasitize multiple hosts simultaneously; thus, they may serve as a common network connecting multiple individuals in a plant community. This function may be somewhat similar to that of hyphal networks of mycorrhizal fungi, which have been shown to convey systemic signals that facilitate community functions such as adaptation to biotic or abiotic stresses (Barto et al., 2012). Recently, these functions have been demonstrated for

BOX 1. ROOT-HEMIPARASITIC RHINANTHUS SPECIES IN ECOLOGICAL RESTORATION.

Rhinanthus species are annual root-hemiparasitic herbs native to western Eurasia. They occur in various types of grasslands where they have been recognized as species that reduce productivity in traditional hay-making agriculture. Ecological research has demonstrated that this reduction of productivity is associated with the decrease of dominance of grasses in the community (Davies et al., 1997; Hartley et al., 2015). As a result, competitively inferior dicot forbs are released from competition and increase in abundance. In parallel, *Rhinanthus* spp. were demonstrated to affect soil properties and processes as well as invertebrate community composition (Bardgett et al., 2006; Hartley et al., 2015). In many cases, the presence of *Rhinanthus* is associated with increased community diversity (Fibich et al., 2017) or abundance of keystone species such as pollinators or invertebrate predators (Hartley et al., 2015). Blossoming forbs and *Rhinanthus* itself also improve the aesthetic impression of the grassland which contributed to a great popularity of *Rhinanthus* spp. as biodiversity-promoting ecosystem engineers (see Figure). Most recently, two *Rhinanthus* species have been demonstrated as efficient in suppressing the native-invader grass *Calamagrostis epigejos* in Central Europe. Expansion of this grass supported mostly by land-use change has been one of the most severe nature conservation issues in the region due to its extent and impact on biodiversity and inefficiency of conventional counter measures. Sowing experiments with *R. alectorolophus* and *R. major* have demonstrated the ability of these two species to suppress *C. epigejos* (Těšitel et al., 2017; Těšitel et al., 2018). Sowing of *Rhinanthus* generally triggered restoration of community composition, and in some cases increased plant diversity or abundance of threatened species. Following this experimental evidence and development of seed-production technology, the use of *R. alectorolophus* has been implemented as a standard measure in nature conservation in the Czech Republic.

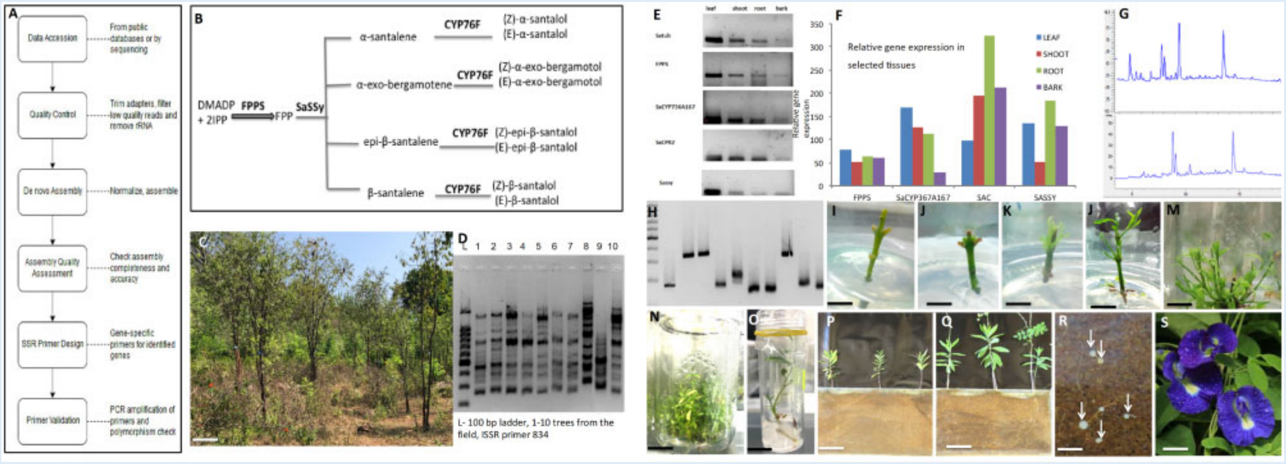
An example of a species-rich meadow patch with *R. alectorolophus* (white arrows) as a result of grassland restoration on ex-arable land.

a stem-parasitic *Cuscuta australis*, which was shown to transfer systemic signals between connected hosts, including warning signals against insect herbivores (Hettenhausen et al., 2017) and salt stress (Li et al., 2020). The warning signals formed by one host plant in response to insect attack or salt stress primed the unattacked/unstressed hosts connected by the *Cuscuta* bridge against subsequent stress induced under greenhouse conditions (Hettenhausen et al., 2017; Li et al., 2020). The transfer of systemic warning signals was shown to be fast (*ca.* 1 $\mathrm{cm \cdot min^{-1}}$) and far-reaching ($>$ 100 cm), and could occur among conspecific or heterospecific hosts from different families (Hettenhausen et al., 2017). Since plant vasculatures were shown to transmit many types of systemic signals induced by various biotic (Fu and Dong, 2013) and abiotic stresses (Schachtman and Goodger, 2008; Chiou and Lin, 2011), vascular connections in plant clusters via *Cuscuta* bridging may facilitate inter-plant communication of multiple stress-induced signals. By

BOX 2. USE OF TRANSCRIPTOMICS FOR BREEDING SUPERIOR SANDALWOOD GENOTYPES.

S. album is among the most valuable trees in the world. Nevertheless, commercial cultivation is limited for several reasons. These include slow growth, variation of oil yield and quality in generatively propagated plants, and a long-time gap between investment into plantation establishment and the revenues from the harvest. A systems biology approach combined with cutting-edge fundamental biology, tissue culture and agronomy was used to solve farmer-level and industrial issues (see Figure). The goal was to identify mother plants providing superior quality oil in large quantity and to develop a micro-propagation protocol for these superior genotypes. Simple sequence repeat (SSR) markers were developed for specific genes in the santalol biosynthesis pathway that are differentially expressed in response to the oil quality and quantity. These genes are differentially expressed in different tissue types of the same plant. The SSR markers were helpful in identification of superior-genotype mother plants in the field. With the development of an efficient tissue culture protocol, a single cutting results in about 1000 plantlets within a year. Additional benefit to the farmer comes from experimental identification of *Clitoria ternatea* as a high-quality host that promotes the early growth of *S. album*.

A, Publicly available RNAseq data were used to assemble the *S. album* transncriptome and a semi-automated system was developed for SSR primer design for specific genes. It can easily be adapted to design SSR primers for breeding programs. B, Several research groups have previously elucidated major steps and genes of the santalol biosynthesis pathway. The major genes of the pathway are dimethylallyl diphosphate (DMADP); isopentenyl diphosphate (IPP); farnesyl diphosphate (FPP); farnesyl diphosphate synthase (FPPS); *S. album* santalene synthase (SaSSy) and several cytochrome P450 (CYP76F) subfamily members. C, *ca.* 10-year-old commercial *S. album* plantation established by seed propagation—the saplings are largely variable despite identical management. D, The genetic variation of 10 seed-propagated plants of the planation (C) assessed at the inter simple sequence region (ISSR). E and F, Differential expression of major genes of the santalol biosynthetic pathway in different tissue types of the same plant (Satub - *S. album tubulin* was used as the internal control). Expression of major genes in santalol biosynthesis is correlated with the quality and quantity of oil. G, High-performance liquid chromatography chromatograms of two representative plants from plantation (C) showing the variation in chemical composition of the stem extracts. H, Gene-specific polymorphic SSR markers to identify plants with high quality and quantity of oil. I–O, Micropropagation process starting from nodal cuttings to rooted plantlets to multiply superior mother plants avoiding genetic recombination associated with seed propagation. P–Q, Identification of superior hosts for early growth in the rhizotrone system, P: without host, Q: with a legume host – *Clitoria ternatea***.** R, Haustoria (marked with white arrows) formed in the rhizotrone system. S, *C. ternatea* flowers have economic value and provide additional income for farmers without affecting *S. album* growth. Size bars: C: 60 cm, I–L: 1 cm, M: 1.5 cm, N: 3 cm, O: 1.5 cm, P–S: 6 cm, R: 1 cm, S: 1.25 cm.



providing information-based benefits, the *Cuscuta* vines might alleviate fitness costs of parasitism to their hosts to some extent (Hettenhausen et al., 2017). At present, the nature of the mobile warning signals and the degree of host and *Cuscuta* control of their delivery remain unknown, as well as the ecological significance of the network in natural environments. Nevertheless, inter-plant communication of warning signals and extensive inter-plant protein transfer with retained biological activities (Liu et al., 2020) in plant clusters connected by *Cuscuta* suggest important roles of parasitic vines in reshaping multitrophic interactions in the infested community.

Harmful effects on host plants may increase community diversity and suppress plant invasions

The effects of parasitic plants at the community scale strongly differ between hosts and non-host plants. The presence of parasitic plants in the community generally alters the competitive balance and influences community structure. Typically, host species are reduced and the free space and resources may be exploited by species resistant or tolerant to parasitism (Marvier, 1998; Joshi et al., 2000; Cameron et al., 2005; Mudrák and Lepš, 2010). Many aspects of plant communities, including diversity or reproduction opportunities, are frequently limited by strong dominance of a single or few species of high competitive ability. In herbaceous vegetation, this applies in particular to communities of high primary productivity (Grime, 1973; Fraser et al., 2015). Parasitic plants were repeatedly demonstrated to reduce growth and competitive ability of dominant species, reduce community productivity and facilitate regeneration from seeds by opening gaps for seedling establishment (Davies et al., 1997; Westbury et al., 2006; Demey et al., 2014; Těšitel et al., 2017). Thus, the general negative effect parasitic plants exert on their hosts may be transformed into positive effects on larger plant community scales (Figure 1).

Empirical evidence of such positive community effects has accumulated mostly for root-hemiparasitic plants over the past *ca*. 20 years. A series of studies demonstrated the positive effects of root-hemiparasitic *Rhinanthus* spp. on diversity of European grasslands (Davies et al., 1997; Bardgett et al., 2006; Westbury et al., 2006; Hartley et al., 2015; Fibich et al., 2017; Box 1). Positive effects on diversity based on competitive dominant suppression were also observed in *Pedicularis palustris* (Decleer et al., 2013) in European wetlands. Facilitation of reproduction of several co-occurring species by improved seedling establishment was demonstrated in a study with hemiparasitic *Rhinanthus minor* and *Pedicularis sylvatica* (Demey et al., 2014). In North American prairies, the presence of two hemiparasitic species *Comandra umbellata* and *Pedicularis canadensis* was found to be positively correlated with community diversity (Sivicek and Taft, 2011), though subsequent experimental research on the ecology of *P. canadensis* identified rather complex effects of this species on diversity (Walder et al., 2019; Borowicz et al., 2019).On top of the positive community effects, several parasitic plants have recently been demonstrated to act as biotic resistance agents against plant invasions (Figure 1). Invasions of alien plants which colonize various natural habitats and suppress native species (Vilà et al., 2011) represent one of the most important threats to biodiversity (Ichii et al., 2019) and compromise human health and food security (Pejchar and Mooney, 2009). Moreover, expansive native species (native invaders) that uncontrollably spread within their natural geographical range and colonize new habitats may negatively impact ecosystems to a similar extent as alien invaders (Nackley et al., 2017). A common feature of invasive plants (alien or native) with strong negative impact on diversity is high biomass production. Growth of these dominant plants may, however, be suppressed by parasitic plants.

A series of recent studies have identified biotic resistance effects (Levine et al., 2004) in several parasitic plants worldwide (reviewed by Těšitel et al., 2020). In particular, three experimental systems studied in sufficient detail demonstrate the suppressive effect of native parasitic plants to alien or native invasive plants. First, the native invader grass *Calamagrostis epigejos* that threatens grassland diversity in Europe was successfully suppressed by *Rhinanthus* species to a degree comparable to or stronger than conventional management (mowing, grazing; see Box 1 for details; Těšitel et al., 2017, 2018). Second, *Cassytha pubescens*, a stem hemiparasite native to Australia, was demonstrated to attack noxious invaders *Ulex europaeus* and *Cytisus scoparius*. Infection by *Cassytha pubescens* reduced its host's maximum electron transport rate and photosystem II efficiency, and thus induced chronic photoinhibition in infected plants (Shen et al., 2010; Cirocco et al., 2018). The observed reduction of host biomass by *C. pubescens* was significantly higher in invasive *Ulex europaeus* and *Cytisus scoparius* than in native hosts (Cirocco et al., 2016, 2017). A field study also identified significantly elevated mortality of invasive *C. scoparius* caused by *C. pubescens* infection in comparison with the native shrub *Leptospermum myrsinoides* (Prider et al., 2009). The third system comprises species of the genus *Cuscuta*, which were tested as possible biological control agents for invasive clonal perennials *Ipomoea cairica*, *Mikania micrantha*, *Wedelia trilobata*, *Solidago canadensis*, *Bidens pilosa*, and *Humulus scandens* in China (Yu et al., 2011; Li et al., 2012; Wu et al., 2019). These alien host species were generally demonstrated to be more vulnerable to parasitic infection than the native ones. In one field experiment, both native species relative abundance and community diversity increased after *Cuscuta australis* established spontaneously (Yu et al., 2011). This empirical evidence demonstrates the potential of parasitic plants to act as biotic resistance agents to plant invasions, though only the *Calamagrostis epigejos*–*Rhinanthus* spp. has hitherto been used in nature conservation/restoration practices. However, such applications of parasitic plants should only consider native species in

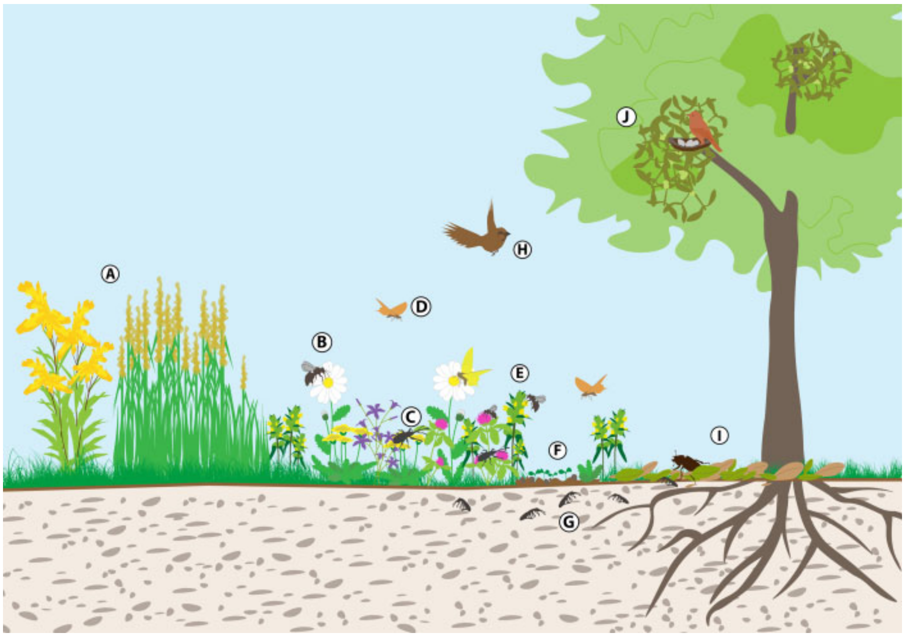


Figure 1 Illustration of functional roles of most significant parasitic plant groups (mistletoes and root hemiparasites) in ecosystems. A, Competitive alien invasive species and native invaders thriving in the absence of parasitic plants. B, Change in the plant community, increasing biodiversity. C, Diversified food supply for herbivores. D, Increased diversity and abundance of pollinators (e.g. Hymenoptera, Lepidoptera, Diptera). E, Root hemiparasite as ecosystem engineer and food opportunity for pollinators and herbivores. F, Sward gap for seedlings establishment. G, Increased soil organic matter and edafauna (Collembola, microorganisms). H, Increased food opportunity for seed herbivores and predators, seed dispersion by herbivores. I, Increased nutrient-rich litter, decompositors, and other animals living in litter. J, Mistletoe – opportunity for nesting, food, shelter.

accordance with biotic resistance theory. Thorough testing in natural community settings should be conducted before any application to identify not only the effects on the target invasive plant but also on the rest of the community. This should minimize possible negative collateral effects occasionally associated with the introduction of a parasitic plant (Walder et al., 2019).

Indirect effects of parasitic plants: enhancing ecosystem processes and providing resources for animal communities

The ecological influence of parasitic plants extends beyond individual hosts and plant communities, having a range of effects that resonate across entire ecosystems and involve higher trophic levels than primary producers (Figure 1; Press and Phoenix, 2005; Watson, 2009). In addition to direct effects mediated by altering competitive dominance of principal hosts discussed in the previous section, indirect effects arise from nutrient reallocation, driven by high rates of enriched litter-fall. Parasitic plants have high fractions of mineral nutrients in their tissues (Quested et al., 2003a; Press and Phoenix, 2005; Gebauer et al., 2012; Fisher et al., 2013; Demey et al., 2014). These nutrients are characteristically not reabsorbed prior to abscission. While most of these nutrients become available to infected hosts (Fisher et al., 2013), they are also accessible to adjacent, uninfected plants. Thus, growth rates of plants growing beneath or beside infected hosts are elevated, a pattern especially prominent in annual and relatively fast-growing plants (Quested et al., 2003b; Watson et al., 2011; Demey et al., 2013). The litter pathway may increase productivity and eventually increase diversity especially in nutrient-poor ecosystems (Spasojevic and Suding, 2011; Griebel et al., 2017), an effect which may extend over several trophic levels of the ecosystem (Watson et al., 2011; Griebel et al., 2017). However, such reallocation may also promote the growth of invasive species (March and Watson, 2010). Some research indicates similar patterns below ground mediated via mycorrhizal networks of fungi that favor infected plants (Mueller and Gehring, 2006). In addition to increased diversity, trees infected with dwarf mistletoes (*Arceuthobium* spp.) were characterized by greater fungal biomass in their root zone, with consequent effects on decomposition and soil structure (Cullings et al., 2005).

Most parasitic plants rely on animals as vectors, thus providing food resources like nectar for pollinators, or fleshy fruit for seed dispersers (Watson, 2001; Bellot and Renner, 2013). In grasslands, the effects of parasitic plants also tend to increase the abundance ratio between insect- and wind-pollinated plants species (Figure 1; Marvier, 1998; Ameloot et al., 2005; Westbury et al., 2006; Bao et al., 2015; Demey et al., 2015). This further enhances food resources for pollinators, but may have a positive cascade effect on the whole invertebrate community (Hartley et al., 2015). In addition, nutrients are imported by visiting pollinators and seed dispersers. For instance, trees infected with mistletoes are visited by more birds which deposit more excreta beneath them (Mellado and Zamora, 2017). Further, many parasitic plants are highly favored food plants for herbivores, especially insects and mammals which may travel long distances in search of their leaves (Petrović, 2014). Given the aggregated distribution that characterizes many parasitic plants, this leads to increased heterogeneity of nutrient availability, with nutrients becoming concentrated beneath heavily infected hosts. Rather than simply reallocation from the host plants themselves, this is also driven by small- to medium-scale nutrient subsidies (Watson, 2016). Along with nutrients, seeds of other plants are brought in (Mellado and Zamora, 2016), resulting in forests with mistletoes progressively becoming more dominated by other plants with fleshy fruits, and in turn, increasing resource availability and dispersal effectiveness for shared seed vectors (van Ommeren and Whitham 2002; Carlo and Aukema 2005).

In addition to affecting the structure and function of plant communities, the combined effect of these direct and indirect effects (known as a facilitation cascade) can alter overall ecosystem structure (Watson, 2016; Thomsen et al., 2018). Given the extended phenology of many parasitic plants, nectar and fruits are available for longer periods of time, allowing populations of pollinators and seed dispersers to become resident (Fonturbel, 2020, and references therein). This is especially the case in lower productivity systems, such as cool temperate forests and arid ecosystems, where root hemiparasites and mistletoe can frequently be the most reliable sources of nectar and fruit (Meidell, 1944; Simpson et al., 1977; Napier et al., 2013).

Human use of parasitic plants and their products

Parasitic plants have long been exploited for human use, including for food, medicine and cultural purposes in human societies worldwide (Kuijt, 1969; Brand-Miller and Holt, 1998; Büssing, 2004). Australia's first nation people, for example, have sustained their well-being for some 50–65,000 years on a diet rich in indigenous flora—including a wide range of parasitic plants, primarily from the Santalaceae, Loranthaceae and Lauraceae families (Brand-Miller and Holt 1998; Clarke, 2008). A very different example is ecotourism recently developed around prominent *Rafflesia* flowers, which contributes substantially to the economies of several South-East Asian regions (Barcelona et al., 2009). The cultural value of parasitic plants is also well known in Europe, where religious use of the mistletoe *Viscum album* has a long history dating back to ancient Greece and the Celtic period (Büssing, 2004). *Viscum album* also played an important role in the Roman legend of Aeneas. The origin of the modern mistletoe tradition relates to Celtic pagan rites of the winter solstice (Paine and Harrison, 2018). Christianity later incorporated it into Christmas celebrations as a symbol of love and protection from evil spirits.

Parasitic plants are widely used in both folk and modern medicines

A great proportion of parasitic plant taxa have been used as folk medicines in various regions around the world, particularly Asia, Europe, and Africa (Figure 2). Parasitic plants from the families Orobanchaceae and Loranthaceae are the most reported medicinal plants, with 52 (from 19 genera) and 22 (from 14 genera) experimentally studied species, respectively. Phenolic compounds (particularly flavonoids), glycosides, alkaloids, and fatty acids are the most frequently reported bioactive phytochemical ingredients in parasitic plants (Figure 2). Compounds from parasitic plants have a wide range of medicinal activities, with antimicrobial (Koch et al., 2009; Moghadamtousi et al., 2014; Chabra et al., 2019), anti-inflammatory (Carrillo-Ocampo et al., 2013; Kim et al., 2016; Park et al., 2018), antioxidative (Cui et al., 2013; Fu et al., 2018), anticancer (Kienle et al., 2009; Alonso-Castro et al., 2012), and neuroprotective properties (Moghadamtousi et al., 2014; Li et al., 2016) being the most frequently reported effects (Figure 2).

Most medicinal parasitic plants are used in regions where they are indigenous. For example, *Cistanche deserticola* (Orobanchaceae), a root holoparasitic herb with a high content of phenylethanoid glycosides, has been used as an anti-aging medicinal plant in China for more than 1,800 years to improve the immune system, enhance kidney and skeletal function, and balance hormones for both men and women (Li et al., 2016; Fu et al., 2018). The mistletoe *V. album* (Viscaceae), a stem hemiparasitic shrub rich in mistletoe lectins and widely distributed in Europe, is a common complementary medicine across Europe for treating breast and gynecological cancers (Kienle et al., 2009). *Cuscuta* (Convolvulaceae) species are used as anti-aging, anti-inflammatory, pain relieving, immune stimulatory, and aphrodisiac agents in traditional medicines to treat a wide range of diseases in Asia (Noureen et al., 2019). *Krameria triandra* (Krameriaceae) root extracts have strong anti-inflammatory effects and photoprotective potential. It is used in European and Euro-American traditional medicines to treat intestinal swelling and skin photodamage (Simpson, 1991; Carini et al., 2002). *Hydnora abyssinica* (Hydnoraceae) rhizomes are used in South African folk medicines against diarrhea, menstrual problems, stomach cramps and intestinal ailments (Williams et al., 2011)

The medicinal properties of many parasitic plants have been validated by phytochemical and pharmacological studies, but knowledge gaps still persist. First, the therapeutic effects of some parasitic plants are still in the exploration stage (Lim et al., 2016). Clinical trials need to be undertaken and mechanisms associated with biological activities of the plants need to be unraveled before their utilization as a source of pharmacological drugs. Second, many medicinal parasitic plants are used as crude extracts with less effective

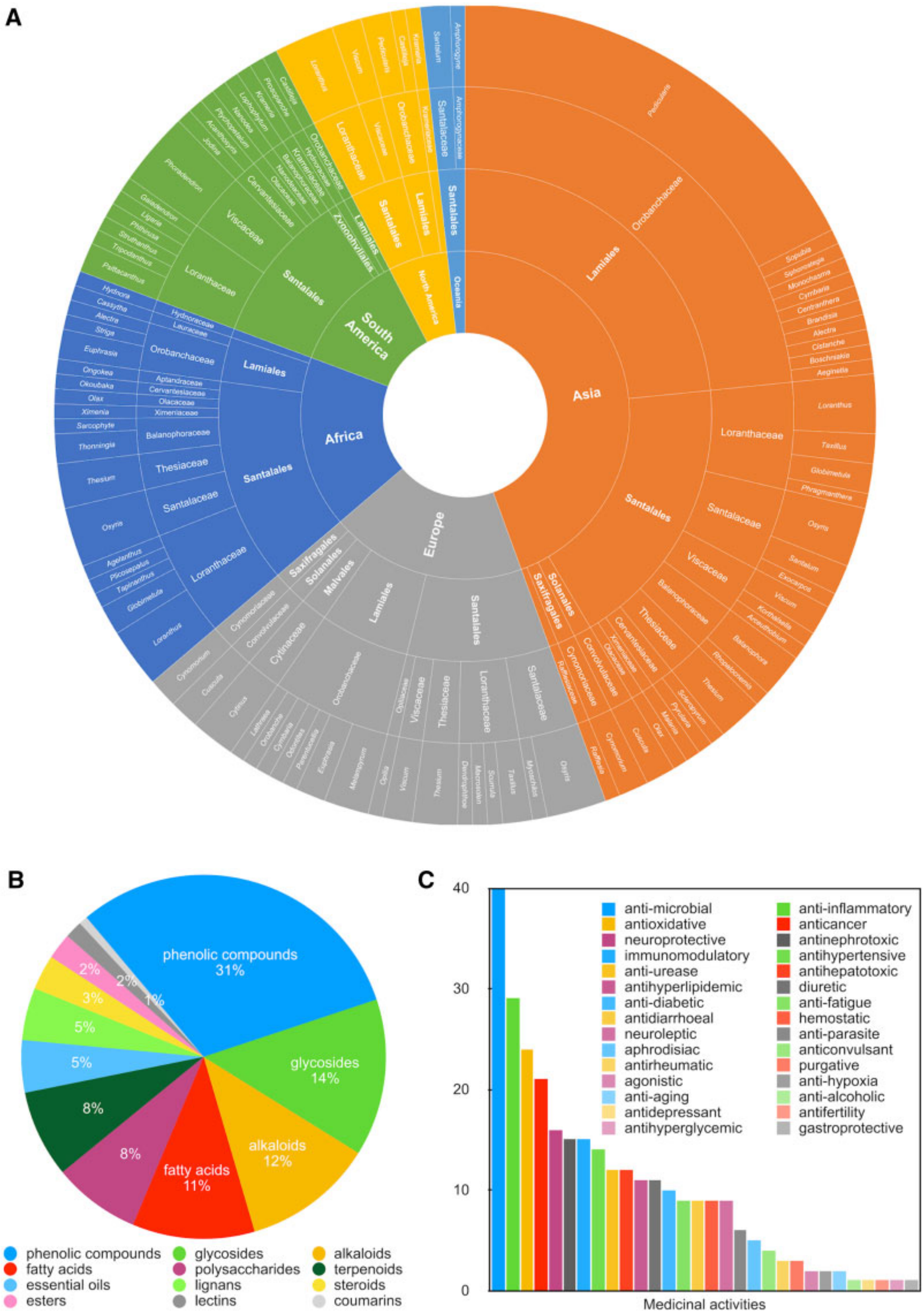


Figure 2 Representative taxa, active compounds, and pharmacological activities of medicinal parasitic plants. A, representative parasitic plant taxa used in various continents. B, primary phytochemical ingredients reported in medicinal parasitic plants. C, medicinal activities reported for parasitic plants.

and nonstandard preparation. Improper preparation of the medicinal plants may result in toxic effects (Ojewole and Adewole, 2007), calling for standardization in drug preparation. Third, lack of knowledge about host dependency and host influence on the phytochemistry and toxicological profile of medicinal parasites may lead to suboptimal quality in terms of medicinal effects (Zorofchian Moghadamtousi et al., 2013), or even fatal consequences (Cheung et al., 2018). Further investigations of variation in phytochemistry and toxicological profiles of the medicinal parasites parasitizing different hosts are thus necessary to appraise their medicinal values.

The genus *Santalum*: parasitic plants exploited and cultivated for their products

Small root-parasitic trees or shrubs of the genus *Santalum* have provided a range of plant products widely used in medicine, cosmetics, and as food on the global scale. A whole series of *Santalum* species is exploited by humans, with *S. album* and *S. spicatum* in particular harvested by means of industrialized production in the tropical and subtropical regions of South Asia and Australia, respectively. (Kuijt, 1969; Venkatesha Gowda, 2011; Teixeira da Silva et al., 2016). Large quantities of *S. album* are currently produced in cultivated plantations in South East Asia and northern Australia. Like virtually all of the world's fragrant sandalwoods, *S. album* has been heavily exploited across its natural range for many years and is now listed as "vulnerable" on the International Union for Conservation of Nature (IUCN) Red List (Arunkumar et al., 2019; IUCN, 2020).

The fragrant *S. album* wood is extensively used to make precious items such as jewelry, jewel cases, boxes, cabinet panels, picture frames, hand fans, pen holders, combs, and letter openers. These items, as well as carvings of gods and mythological figures, command high prices in local and international markets. Nevertheless, the principal *S. album* product is the valuable aromatic sandalwood oil which is extracted by steam distillation from the heartwood of *S. album*, the only part of the tree carrying the fragrance (Srinivasan et al., 1992). The oil is a pale yellow, somewhat viscous liquid consisting almost entirely of closely related sesquiterpenoids, particularly alpha-santalol (which comprises approximately 7%–60% of total santalol), and beta-santalol (comprising approximately 7%–33%; Lawrence, 1991). Sandalwood oil is an essential component of many perfumes as it is not only aromatic in itself, but also helps to carry the fragrance of other flowers and herbs (Kumar et al., 2012). The oil is also used in medicine to treat a range of ailments including the common cold, bronchitis, fever, dysentery, piles, scabies, urinary infections, and several other organ complications (Ochi et al., 2005). Research has identified a range of properties of sandalwood oil and its constituents behind these uses, including anti-fungal (Warnke et al., 2009), antiviral against drug-resistant herpes simplex virus (Schnitzler et al., 2007), anti-carcinogenic (Burdock and Carabin, 2008), and anti-influenza HK (H3N2) anti-viral capacities (Paulpandi et al., 2012). *S. album* oil was also recorded as helping to address pulse rate issues, skin conductance, and cytosolic blood pressure (Heubeger et al., 2006). *S. album* exploitation and use is part of a long and rich cultural heritage that dates back some 5,000 years and is even mentioned in the ancient Sanskrit manuscripts (Flansda, 2009). Ancient Egyptians are known to have imported the wood for medicinal use, as well as for use in preservation, and for ritual burning to worship their gods (Arctander, 1960). The oil and wood of *S. album* (and *S. spicatum*) are used for religious purposes in three of the world's major religions: Hinduism, Buddhism, and Islam (Kumar et al., 2012). Hindu people believe the goddess Lakshmi resides in the *S. album* tree (Sensarma, 1989) and use the wood to worship the god Shiva. In Buddhist rituals, the fragrant sandalwood is burnt during worshipping and meditation, and even the sapwood is used––for cremations, and for making offerings at temples.

Several other *Santalum* species are used in Australia. *Santalum acuminatum*, known as "Quandong", is a small hemiparasitic tree that grows throughout southern Australia. It bears large, nutritious, bright-red drupes when ripe, which are considered pre-eminent among Aboriginal peoples' "bush-foods" (Low, 1988; Pardoe et al., 2019). Referred to as a "super food", it has been treasured, traded, and transported for millennia (Fuentes-Cross, 2015; Lullfitz, 2017). Rich in energy, protein, fat, minerals, and vitamins (it has twice the level of Vitamin C than oranges), Quandong fruit is considered a staple for Aboriginal people, and is eaten raw or roasted, or rolled into cakes or balls before being dried and stored for later consumption (Meagher, 1974; Brand-Miller and Holt, 1998; Newton, 2016). Partly due to its rich antioxidant and antibacterial characteristics (Zhao and Agboola, 2007), *S. acuminatum* has also been used for a range of medicinal purposes, with its fruit, kernel, leaves, roots, and bark all applied to treat a variety of health issues from skin disorders and venereal disease, to rheumatism and muscular complaints. A number of other Australian *Santalum* species have been used as indigenous bushfood or bush-medicine (Karadada, 2011, Fuentes-Cross, 2015). Australian Sandalwood (*Santalum spicatum*) has predominantly been used for medicinal and spiritual purposes, with its oil-rich seeds (as well as its leaves, branches and trunks) being applied to a variety of medicinal ailments (including the treatment of skin afflictions, cuts, infections, sores, burns, colds, and stiffness), as well as being burned in ceremonies or for individual's spiritual well-being (Meagher, 1974). Its timber, rich in sandalwood oil, is still being exploited in the wild and currently meets about 40% of the world's sandalwood timber demand (Tonts and Selwood, 2003). Northern Sandalwood (*Santalum lanceolatum*) and Bitter Quandong (*Santalum murrayanum*) have also been used for a variety of purposes (Maiden, 1889; Low, 1988). Other parasitic plants used for bush food and bush medicine by Australia's Indigenous people include species of the genera *Exocarpos*, *Leptomeria*, *Amyema*, *Lysiana*, *Cassytha*, and *Nuytsia* (Maiden, 1889; Meagher, 1974; Low, 1988). Newton (2016) refers to them as "the oldest foods on Earth".

Parasitic plants are subject to agronomy and forestry cultivation

Attempts have been made worldwide to cultivate useful local parasitic plants for timber, foods, medicines, or industrial uses. Reported parasitic plants in cultivation include but are not limited to *Anacolosa frutescens* (as nut trees), *Melientha suavis* (for vegetables and fruits), *Arjona tuberosa* (for edible tubers), *S. acuminatum* (for fruits), *S. album* (for essential oil), *Ximenia americana* (for edible fruits and seeds), *Orobanche crenata* (as vegetables and medicinal plants), *V. album* (for medicinal uses), and *Euphrasia officinalis* (for medicinal uses; Pignone and Hammer, 2016). Large plantations have been established for a couple of parasitic plants with high economic values

Figure 3 Cultivation of parasitic plants with high economic values promotes ecological services. A–B, A sandalwood (*S. album*) resort area in southern China, photos by Guohua Ma. C, Reforestation using *Malania oleifera* in karst regions of southwestern China. D, Grassland restoration using *Rhinanthus alectorolophus* in Czech Republic, photo by Stanislav Hejduk. E, Desert revegetation with root holoparasitic *Cistanche tubulosa* and its host *Tamarix chinensis* in northwestern China, photo by Pengfei Tu. F, Desert revegetation with root holoparasitic *Cistanche deserticola* and its host *Haloxylon ammodendron* in northeastern China, photo by Pengfei Tu. G, *Santalum acuminatum* in fruit in Southern Australia, photo by Richard McLellan

(Figure 3). Apart from providing great economic profits, plantations of parasitic plants play important roles in enhancing ecological revegetation, hence increasing the provision of ecosystem services. *Santalum* species (particularly *S. album* and *S. spicatum*) are the most prominent root hemiparasitic trees being widely planted for precious sandalwood oil in several countries (e.g. Australia, India, China, Indonesia, Malaysia, and Sri Lanka) with modern breeding and propagation technologies greatly enhancing the cultivation efficiency (Box 2). In southern China, plantation of *S. album* on a large scale began in 2013 and reached 5,000 ha in 2016 with a rapid expanding rate, mainly in mountainous areas (Teixeira da Silva et al., 2016). Recently, great efforts have also been made to grow *Malania oleifera*, another root hemiparasitic tree species indigenous to karst areas in southwestern China (Li et al., 2019), which is valued not only for high nervonic acid content in seeds (Ma et al., 2004; Tang et al., 2013), but also for its great potential in forest restoration in karst regions (Lü et al., 2016). *Cistanche deserticola* and *C. tubulosa*, herbaceous root holoparasites with high medicinal values (Li et al., 2016; Fu et al., 2018), have been planted at large scales in desert regions in Northern China. Since these valuable holoparasites show optimal growth only in sandy soil in arid regions, motivation to establish *Cistanche* plantations using host plants good for desert revegetation have been increasing. It is estimated that plantation of *C. deserticola* and *C. tubulosa* have so far contributed to desert revegetation of more than 40,000 ha by motivating people to grow desert shrubs as their host plants. Due to their great adaptation to disturbed and nutrient-poor habitats, more parasitic plants are becoming incentives for ecological revegetation in regions where revegetation efforts are otherwise scarce.

Figure 4 High aesthetic values of parasitic plants, which are used or are suitable for use in horticulture. A–C, Himalayan *Pedicularis* species (*P. olivcriana*, *P. oxycarpa*, and *P. tricolor* from left to right). D, *Nuytsia floribunda*, photo by Owen Roberts. E, *Melampyrum arvense*. Photo by Jakub Těšitel. F, *Castilleja latifolia*, photo by Huiting Zhang. G, *Taxillus delavayi*, photo by Yang Niu

Aesthetics of parasitic plants in horticulture

Many parasitic plants show great aesthetic value with striking colors, unusual corolla shapes, showy fruits, or other unique morphologies, giving them great potential for application in landscape architecture and planting design (Figure 4). Still, horticultural uses of parasitic plants are scarce. The general impression that parasitic plants are harmful may have discouraged people to grow parasitic plants in their gardens. Another likely reason is the complexity in cultivation of parasitic plants, optimal performance of which depends on not only host identity but also on various environmental factors (Gawler et al., 1987; Mellado and Zamora, 2014; Liu et al., 2017). Nevertheless, with increasing demand in diverse horticultural industries, the most underutilized parasitic plants may serve as valued resources for novel horticultural plants, thanks to their unique characteristics and intriguing biological traits.

Current trends in horticulture are focused on naturalistic planting design, self-regulation, diversity and ecological functionality (Dunnett, 2019; Oudolf and Kingsbury, 2013). With wide distribution, high diversity, and great potential as ecosystem engineers, parasitic plants are definitely included in new horticulture ideas. Landscape architecture can use parasitic plants as a cheap and ecological autoregulation mechanism to improve aesthetic value, diversity and to reduce maintenance of present lawns. Root hemiparasitic *Rhinanthus minor* was used this way in the United Kingdom (Pywell et al., 2004; Westbury et al., 2006). A promising use of hemiparasitic plants in designed meadows was performed by Hitchmough (2017) and his colleagues in Great Britain who demonstrated successful cultivation of the appealing American root hemiparasites *Castilleja coccinea* and *C. integra* with common garden plants like *Penstemon* species or *Phlox* species as hosts. Sowing mixtures for semi-natural meadows including root-hemiparasitic *Melampyrum arvense* were tested in Austria (Brocks et al., 2016). Efforts have also been taken in China for horticultural cultivation of *Pedicularis* species (Li et al., 1997; Wang and Tang, 2005; Li and Guan, 2007), a large group (*ca.* 800 species worldwide) of root hemiparasitic plants with interesting flowers of high morphological diversity.

Some parasitic plants may also be used in floral design, though with some limits such as limited shelf life due to fast water loss because of high transpiration rates by nature (Stewart and Press, 1990). The most popular and commonly used parasitic plants for decoration are stem hemiparasitic mistletoes (*Viscum*, *Phoradendron*; Paine and Harrison, 2018). Apart from Christmas season decorations, modern use of mistletoe as a wedding decoration or a bouquet element can be interesting and promising. Wood roses also represent mistletoe-related products used for ornamental purposes. They are not formed by mistletoes themselves but consist of proliferated host tissue typical of haustorial attachments of some African and American *Loranthaceae* (Mathiasen et al., 2008; Dzerefos et al., 2009).

Conclusions and risk assessment

Naturally growing parasitic plants should primarily be regarded as an important functional component of terrestrial ecosystems. Many parasitic plant species may have positive effects on biodiversity across multiple groups of organisms. Available empirical evidence points particularly to the effects of root hemiparasites and mistletoes. This evidence is, however, still limited both taxonomically and geographically. Broadening this scope by including other parasitic plants and their host associations in hitherto underinvestigated areas (e.g. mistletoes in tropics, and root hemiparasites in alpine systems and tropical savannas) may thus reveal additional fascinating ecological stories.

Human use of parasitic plants has a long history, but novel applications have emerged in recent years thanks to intense research. In particular, the use of parasitic plants in ecological restoration, invasive plant suppression and horticulture seem promising. Additional research is, however, still required to optimize the methodical approaches and application protocols (see Outstanding questions). This also applies to more traditional medicinal use of parasitic plants.

In this paper, we highlighted the bright side of parasitic plants, but it is important not to forget about their dark side. Therefore, all applications of parasitic plants should undergo a detailed risk assessment, which is crucial in large-scale or uncontrolled applications like agricultural production of commodities, ecological restoration and horticultural use. Invasions of weedy parasitic plants into new areas are well known (Parker, 2013). Similarly, non-weedy parasitic plants beneficial for biodiversity in their native range may spread as alien invaders and cause harm to ecosystems in other parts of the world (van Hulst et al., 1987; Kennedy, 2011). Therefore, we strongly advocate against introductions of parasitic plants outside their native range. This should apply also on horticultural use because many serious plant invasions have started from gardens (Reichard and White, 2001). For instance, we strongly advocate against the suggestion to use the noxious weed *Striga hermonthica* as a possible ornamental plant for Europe (Gladis et al., 2000) but also express concern on the use of American *Castilleja* species in European ornamental horticulture (Hitchmough, 2017). Instead, we believe that research should aim at revealing the potential of indigenous parasitic plants for such applications. Nevertheless, even using native parasitic species is not risk-free. Dangerous pests, like *Striga hermonthica*, *Arceuthobium* spp., *Seymeria cassioides*, or recently emerged *Rhamphicarpa fistulosa* are harmful in agroecosystems or production forests and also within in their native range. Therefore, the risk assessment should be based on detailed knowledge of biology and ecology of specific parasitic plant species.

OUTSTANDING QUESTIONS

- May ecological agriculture and landscape design benefit from the community and ecosystem effects of parasitic plants?
- What are the long-term effects of parasitic plants on soil permeability and carbon sequestration?
- May improved use of genetic resources and plant breeding techniques contribute to more efficient use of parasitic plants as ecosystem engineers?
- How to standardize utilization of parasitic plants as medicinal resources?

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