Mycorrhiza (2008) 18:429–436
DOI 10.1007/s00572-008-0196-z

ORIGINAL PAPER

Arbuscular mycorrhizal fungi may serve as another nutrient strategy for some hemiparasitic species of *Pedicularis* (Orobanchaceae)

Ai-Rong Li · Kai-Yun Guan

Received: 10 May 2008 / Accepted: 29 July 2008 / Published online: 15 August 2008

Abstract As an important component of plant kingdom, parasitic plants have intrigued many scientists with their heterotrophic strategy. Numerous investigations have been carried out for a better understanding of interactions between parasitic plants and their hosts. Nevertheless, studies on parasitic plants from a mycorrhizal perspective are lacking, largely because of the notion that parasitic plants do not form mycorrhizal associations. Although long being regarded as nonmycorrhizal, some *Pedicularis* species are recently found to be heavily colonized by mycorrhizal fungi. Because the precise information about parasitism of Chinese *Pedicularis* has been lacking, we surveyed both the mycorrhizal status and parasitism of 29 *Pedicularis* species from the northwest of Yunnan Province, China, to test the hypothesis that some *Pedicularis* may be mycorrhizal and parasitic simultaneously. The majority of studied species were found to be parasitic as well as mycorrhizal. In some cases, parasitic organs and arbuscular mycorrhizal fungi (AMF) were detected in the same rootlets. The results suggest that some *Pedicularis* species may have another nutrient strategy (e.g., mycotrophy) besides being parasitic. Also, the findings indicate that host plants as well as AMF should be taken into account in cultivation of *Pedicularis* species.

Keywords Arbuscular mycorrhizal fungi (AMF) · Haustoria · Nutrient strategy · Orobanchaceae · Root hemiparasites

Introduction

Parasitic plants are common in many natural and semi-natural ecosystems, comprising more than 1% of terrestrial plant species and having various life forms (Phoenix and Press 2005; Press and Phoenix 2005). Parasitic plants vary a lot in the extent to which they are dependent upon their host plants (Marvier and Smith 1997). However, all parasitic plants are characterized by developing parasitic organs called haustoria, through which organic and/or inorganic nutrients and water are absorbed from host plants. With regard to parasitic plants, the vast majority of studies have been restricted to interactions between hosts and parasites and issues regarding multi-species interactions have been seldom addressed. Of these, a significant yet poorly known aspect of parasitic plants is their interactions with microorganisms (Nickrent 2002).

Mycorrhizal fungi are a main component of the soil microbiota in most ecosystems, and it is believed that a majority of terrestrial plants are associated with some kinds of mycorrhizal fungi, with arbuscular mycorrhizal fungi (AMF) as the most common group (Smith and Read 1997). Accumulating evidence has shown that mycorrhizal fungi play a significant role in nutrient acquisition and nutrient cycling (Francis and Read 1984; Moora and Zobel 1996; Walter et al. 1996; Watkins et al. 1996; Simard et al. 1997; Marler et al. 1999). Nevertheless, owing to the notion that lineages of parasitic plants are nonmycorrhizal (Atsatt 1973; Brundrett 2002), studies on the interactions between mycorrhizal fungi and parasitic plants are scarce. In contrast to countless studies on mycorrhizal associations of autotrophic angiosperms, there are only a few specific investigations concerning the mycorrhizal status of parasitic plants (Lesica and Antibus 1986; Khalid and Iqbal 1995; Chen and Guan 2001; Li and Guan 2007). So far as we know, no

A.-R. Li · K.-Y. Guan (✉)
Kunming Institute of Botany, Chinese Academy of Sciences,
134 Lan-Hei Road,
Kunming, Yunnan 650204, People's Republic of China
e-mail: guanky@mail.kib.ac.cn

effort has yet been taken to study the relations between parasitic plants and their symbiotic fungi.

The genus *Pedicularis* L. (Orobanchaceae) was thought to be nonmycorrhizal (Harley and Harley 1987). However, some species were recently suggested to be colonized by mycorrhizal fungi (Kohn and Stasovski 1990; Väre et al. 1992; Treu et al. 1996; Chen and Guan 2001; Cripps and Eddington 2005). In a survey of the mycorrhizal status of some *Pedicularis* species from Yunnan Province, China, we found that most of our studied species were heavily colonized in the wild by mycorrhizal fungi (mainly AMF; Li and Guan 2007). The high mycorrhizal colonization levels led us to postulate whether these Chinese *Pedicularis* species have a parasitic habit or not.

Pedicularis is a genus consisting of about 600 species, of which the majority were regarded as root hemiparasites (Yang et al. 1998). Although *Pedicularis* species have long been known as hemiparasites, only a few have actually been experimentally examined for their parasitic habit (Piehl 1963; Lackney 1981; Weber 1987; Schneider and Stermitz 1990). Therefore, the viewpoint that most *Pedicularis* species are root hemiparasites is merely a deduction based on the observation of a minority of species. Considering the absence of precise information about parasitism of Chinese *Pedicularis*, it is necessary to verify the parasitic habit of these species. If these species are parasitic as well as mycorrhizal, such information will be valuable for a better understanding of multi-species interactions involving hemiparasitic plants. Moreover, potentially alternative adaptation strategies as being either parasitic or arbuscular mycorrhizal may intrigue ecologists to reach further when considering issues about hemiparasitic plants. Also, cultivation of *Pedicularis* may be expected to gain some success by taking beneficial microorganisms (such as AMF) into account, which has been overlooked in cultivation of these plants (Li and Guan 2007).

In the present study, we attempt to shed some light on the two seemingly alternative nutrient strategies of *Pedicularis* species by addressing the following questions: (1) are the species investigated hemiparasitic? (2) Are the hemiparasitic species colonized by AMF? (3) Is being parasitic a conflict with being mycorrhizal?

Materials and methods

Root sampling and site description

Twenty-nine species (subspecies or varieties; Table 1) representing all the four major evolutionary corolla types described in Li's system (1951) were collected from the northwest of Yunnan Province, mainly from Dali (99°58′–100°27′ E and 25°25′–25°58′ N), Lijiang (99°23′–101°31′ E and 25°59′–27°56′ N) and Zhongdian (also known as Shangrila, 90°35′–100°19′ E and 26°52′–29°16′ N) in August 2004, June 2005, and August 2005. Annual mean temperatures for the three areas are 15.1°C, 12.6°C, and 5.4°C, and annual average rainfall values are about 1,079, 1,000, and 634 mm, respectively. The dominant vegetation consists of grasses, forbs, and/or shrubs in the majority of sampling sites.

For each species, at least three individuals were randomly collected and their entire roots cut for further examination of parasitism and mycorrhizal colonization. During excavation, large clods of earth were dug out to reduce the damage to the rootlets. Root samples were put into formalin–acetic acid–alcohol fixative immediately after removed from soil.

Identification of *Pedicularis* species

Identification of *Pedicularis* species was conducted based on morphological characteristics according to Flora Reipublicae Popularis Sinicae (Tsoong 1963) and Flora of China (Yang et al. 1998). The voucher specimens are deposited in the Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences.

Preparation of root materials

Prior to examination under a dissecting microscope, the root samples were soaked in water for 4 h, then adhering soil particles were carefully removed with the aid of a dissecting needle. Intact root samples were examined under a dissecting microscope for determination of parasitism of the studied *Pedicularis* species. For a better observation of haustorial structure, several typical root samples were processed and stained with trypan blue identically to the procedures for mycorrhizal examination. Only rootlets less than 2 mm in diameter were picked out for examination of mycorrhizal status. The samples were processed according to the method of Phillips and Hayman (1970) with slight modification (Li and Guan 2007). All microscopical determinations were made at ×200 magnification using an Olympus optical microscope. Micrographs were recorded at ×80, ×100, or ×1,000 magnification on an Olympus or Nikon digital microscope camera.

Determination of parasitism and arbuscular mycorrhizal colonization of *Pedicularis* species

Parasitism of the studied species was determined by the presence of haustoria on roots (Estabrook and Yoder 1998; Elias et al. 2001). However, the absence of haustorium in collected sample plants of a species is not definitive proof

Table 1 Parasitism and arbuscular mycorrhizal colonization status of 29 *Pedicularis* species from the northwest of Yunnan Province, China

Pedicularis species	Parasitism and AM status						Colonization level by AMF		
	E	LH	P	AM	MT	FS	NFC/TNFE	F%	CI
P. axillaris Franch.	+	P	+	±	?	H	3/7	42.9	12.4
P. bietii Franch.	+	?	+	±	?	H	11/25	44.0	24.0
P. cephalantha Franch. var. *cephalantha*	+	P	+	+	?	H, V	23/24	95.8	56.9
P. cephalantha var. *szetchuanica* Bonati	+	P	+	+	A	H, A, V	10/22	45.5	36.8
P. cymbalaria Bonati	+	A or B	+	+	P	H, V, HC	23/36	63.9	27.8
P. deltoidea Franch.	+	A or B	+	+	A	H, S, A, V	4/14	28.6	14.3
P. densispica Franch.	+	A	+	+	A	H, V, A	37/41	90.2	58.3
P. dichotoma Bonati	+	P	+	+	?	V, H	16/44	36.4	27.5
P. gracilis Wall.	+	A	+	+	P&A	H, A, HC, V	64/68	94.1	76.4
P. gruina Franch.	+	P	+	−	−	−	0/9	0	0
P. likiangensis Franch.	+	P	−	−	−	−	0/20	0	0
P. longiflora Rudolph	−	A	+	+	?	H, V	25/40	62.5	40.0
P. longipes Maxim.	+	P	+	+	A	H, A, V	7/9	77.8	28.5
P. lutescens Franch. subsp. *lutescens*	+	P	+	+	?	H, V	32/47	68.1	38.3
P. lutescens subsp. *ramose* P. C. Tsoong	+	P	+	+	?	H, V	10/18	55.6	30.6
P. oxycarpa Franch.	+	P	+	+	?	H, V	35/65	53.8	31.3
P. pseudomelampyriflora Bonati	+	A	-	+	?	H, S, V	25/27	92.6	78.0
P. ramosissima Bonati	+	A	+	−	−	−	0/11	0	0
P. rex C. B. Clarke	−	P	+	+	A	H, S, A, V	113/142	79.6	61.0
P. rhinanthoides Schrenk	−	P	-	+	?	H, V, S	7/11	63.6	31.0
P. rhodotricha Maxim.	+	P	+	+	?	H, V	8/13	61.5	36.5
P. salviaeflora Franch.	+	P	+	+	P	H, S, V, HC	21/21	100.0	92.9
P. sigmoidea Franch.	+	P	−	+	A	H, S, A, V	8/8	100.0	100.0
P. siphonantha Don	-	P	+	+	P	H, S, V, HC	50/89	56.2	46.1
P. stadlmanniana Bonati	+	P (?)	+	+	?	H, V	17/20	85.0	66.0
P. tapaoensis Tsoong	+	P	−	+	?	H, V	7/18	38.9	7.1
P. tenuisecta Franch.	+	P	+	+	P	H, V, HC	30/43	69.8	38.0
P. tricolor Hand.-Mazz.	+	P	+	±	?	H	14/21	66.7	36.6
P. yui Li	+	B (?)	+	+	?	H, V	9/17	52.9	38.2
Total	25/29		24/29	(23+3)/29			609/930		

E Endemism: "+" endemic to China, *LH* life history: *A* annual, *B* biennial, *P* perennial, "?" lack of clear description in literature, *P* parasitism of tested *Pedicularis* species: "+" parasitic, "−" occasionally nonparasitic, AM status: "+" mycorrhizal, "±" possibly mycorrhizal, "−" nonmycorrhizal, *MT* morphological type of AM: *A Arum*-type, *P Paris*-type, "?" uncertainty, *FS* detected fungal structure: *H* hypha, *S* spore, *V* vesicle, *A* arbuscule, *HC* hyphal coil, *NFC* number of fragments colonized by AMF, *TNFE* total number of fragments examined, *F%* frequency of colonization, *CI* colonization index.

of being nonparasitic for the species, which is particularly true when the sample size is small. Therefore, if at least one haustorium was observed on any root of a species, this species was considered as parasitic and recorded as "+," while species without trace of haustorium on any sample roots were considered occasionally non-parasitic and recorded as "−."

According to previous studies, defense response of host plants plays a key role in the success of a parasitic plant (Cameron et al. 2006; Cameron and Seel 2007; Rümer et al. 2007). Most haustoria formed on non-host plants are poorly differentiated and, thus, not actually functional in nutrient acquisition (Cameron et al. 2006). The structure of a haustorium differs also at different developmental stages (Cameron and Seel 2007). Therefore, we cannot assert a haustorium we observed as "functional" or "nonfunctional" without experimental evidence. To be cautious, we describe haustoria with xylem bridge as "presumably functional" in this article based on previous findings that such haustoria are generally functional in inorganic nutrients and water transfer (Heide-Jorgensen and Kuijt 1995; Yoder 1997; Cameron et al. 2006; Cameron and Seel 2007).

Mycorrhiza types were designated according to Harley and Smith (1983), and determination of morphological types of AM was only based on the presence of arbuscules or hyphal coils, since it is difficult to determine whether the hyphae are intercellular or intracellular without anatomical examination. If at least one root segment was found to contain arbuscules or hyphal coils or vesicles, then the species was noted as an AM plant, recorded as "+." If the root cortex was found to be colonized by aseptate fungal hyphae but no arbuscules or hyphal coils or vesicles were observed, the corresponding species was noted as possibly AM, recorded as "±." Species were recorded as non-mycorrhizal and presented as "−" when neither arbuscules or hyphal coils or vesicles nor aseptate fungal hyphae were detected in their root cortical cells. AM with arbuscules were recorded "A" (*Arum*-type), and those with hyphal coils were recorded "P" (*Paris*-type).

Determination of AM colonization level

Colonization level of AMF were obtained with colonization frequency (*F*%, percentage of colonized fragments) and colonization index (CI, a parameter representing both colonization frequency and colonization level of individual fragments) as described by Li and Guan (2007).

Results

The overall frequency of parasitism and mycorrhizal level was very high across the studied species (Table 1). Twenty-four out of the 29 studied *Pedicularis* species were found to have developed haustoria. Almost all species were observed to associate with AMF. Among the 29 species, 23 species were determined to be mycorrhizal by AMF and three were found to be possibly colonized by AMF. More than two thirds of the mycorrhizal species have a colonization frequency higher than 50%, and colonization index of eight species are above 50 (Table 1).

We noticed that not all *Pedicularis* plants needed a host plant nearby to survive, even for the species that could develop presumably functional haustoria, namely with a xylem bridge, such as *Pedicularis dichotoma* Bonati. During the fieldwork, a plant of this species was found at a fruiting period without any potential host plants within its reach, and no roots of any other plants were detected nearby by excavation. The absence of potential host plants was also observed for plants of other *Pedicualris* species at various growing stages.

Among the observed haustoria, most were found to develop xylem bridges (Fig. 1a), which connect the parasites and host plants. However, some were found to form only structures similar to those of haustoria but without the formation of a xylem bridge (Fig. 1b).

As to the fungal structures, vesicles were the most frequently encountered and the most abundant structures in the studied species (Fig. 2), being detected in all mycorrhizal species, except for three possibly mycorrhizal species (*Pedicularis axillaries* Franch., *Pedicularis bietii* Franch., and *Pedicularis tricolor* Hand.-Mazz.), from whose roots the only fungal structures detected were aseptate hyphae (Table 1). Intraradical and extraradical hyphae were also frequently observed. Intraradical and extraradical spores were occasionally detected in several species. Arbuscules or hyphal coils were only found in less than half of the checked species. All structures varied in shape and size, even in the same *Pedicularis* species.

Both major AM morphological types, i.e., *Arum*- and *Paris*-types, were observed in the genus *Pedicularis* (Table 1 and Fig. 3). Six species developed only *Arum*-type mycorrhizas and four formed only *Paris*-type associations. One species (*P. gracilis* Wall.) was found to form both *Arum*- and *Paris*-types associations. The morphological types of other species were hard to determine due to the absence of characteristic structures (such as arbuscules and hyphal coils).

Among the examined root materials, coexistence of haustoria and AMF in the same root was rather common. In some cases, mycorrhizal fungi were detected right in the haustoria (Fig. 1).

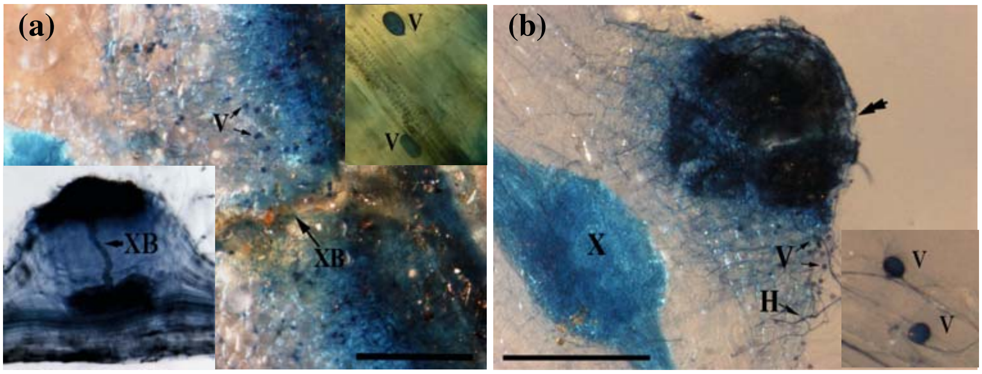

Fig. 1 Coexistence of parasitic organ (haustorium) and AMF in the same rootlet of *Pedicularis*. **a** Vesicles detected in presumably functional haustorium (with xylem bridge) of *P. longipes*. *bar* 100 µm. The *inset at the left bottom* is the stereomicrograph of a cleared haustorium of *P. longipes* and the one on the *right top* is a magnified image of vesicles detected in the haustorium. **b** Vesicles and hyphae observed in haustorium-like structure (without xylem bridge) of *P. salviaeflora*. *bar* 100 µm. The *inset at the right bottom* shows vesicles in roots of *P. salviaeflora* at a higher magnification. *H* hyphae, *V* vesicles, *X* xylem, *XB* xylem bridge

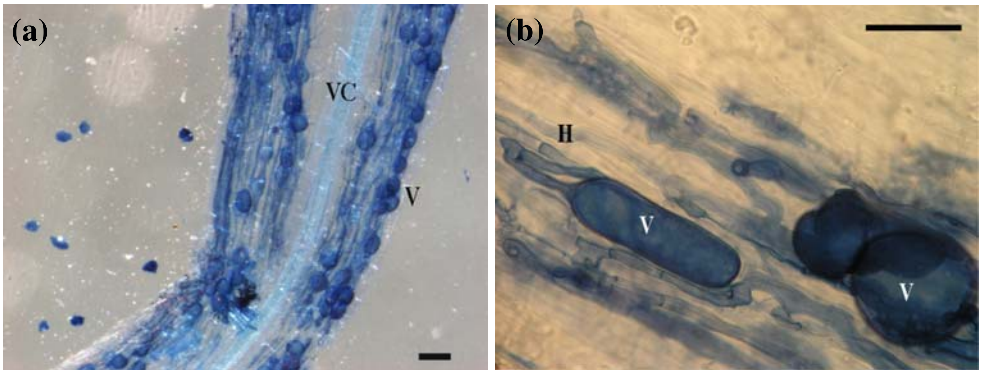

Fig. 2 Vesicles of AMF in roots of *Pedicularis* species. **a** Vesicles detected in roots of *P. rex bar* 80 µm. **b** Vesicles in root cortex of *P. siphonantha bar* 40 µm. *H* hyphae, *V* vesicle, *VC* vascular cylinder

Discussion

We did not find any evidence for parasitism or mycorrhizal colonization in only a small number of species. The vast majority of *Pedicularis* species studied were either parasitic or mycorrhizal, with 19 of the 29 species studied being both parasitic and mycorrhizal. The results need to be interpreted with caution. According to our previous analysis, intraspecific variation exists in terms of mycorrhizal colonization of *Pedicularis* species in different sampling sites (Li and Guan 2007). Thus, based on our limited database, we cannot make the assertion that the nonmycorrhizal species in our survey are free of mycorrhizal associations by nature. Similarly, the lack of parasitism in a few species may be due to a relatively small sample size. By this token, co-occurrence of parasitism and mycorrhiza in *Pedicularis* may be more common than what our data show.

Pedicularis has been known for the complex difficulties encountered in cultivation due to the unknown limiting factors for its cultivation (Li and Guan 2007). Previous studies used to focus on the interactions between *Pedicularis* and its host plants, which have not proven successful. The high frequency of AM associations in 26 out of 29 *Pedicularis* species studied, of which the majority were found to be parasitic, strongly suggests that not only host plants but also AMF should be seriously considered in cultivation of these plants.

It was suggested that there would be very few exceptions to the rule that members of a single plant genus form only one AM morphological type (Smith and Smith 1997). However, according to our observations, different types may form in the genus *Pedicularis*, even in a single species (e.g. *P. gracilis*). This agrees with Kubota et al. (2005) who reported that both *Arum*- and *Paris*-types were detected in the same root systems of test cucumber and tomato species. With regard to controlling factors of the morphology of AM associations, some have suggested that it could be related to plant taxa (Gerdemann 1965; Smith and Smith 1997), whereas others have argued that fungal identity may also play an important role in controlling morphological types of AM (Cavagnaro et al. 2001). Although our study was not designed to address such an issue, the observation of two AM morphological types in a single species may indicate to some extent that formation of certain morphological type is the result of interplay between both the plant and the fungal identity (Cavagnaro et al. 2001). Also, environmental factors may play a role (Yamato 2004).

Undergoing a preparasitic phase prior to the development of functional haustoria is a common phenomenon for hemiparasitic angiosperms, which can last for up to several months (Seel et al. 1993). So, the discovery of *Pedicularis* plants growing independently under field conditions is indeed nothing unusual. Something unusual is the coexistence of mycorrhizal fungi and haustoria in the same

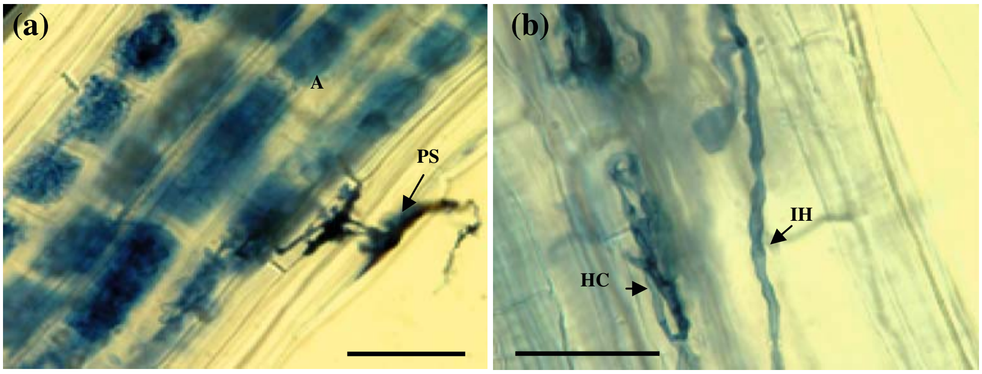

Fig. 3 Two morphological types of AM observed in roots of *Pedicularis* species. **a** *Arum*-type AM: part of a colony of an AM fungus resulting from growth of arbuscules from a single penetration site in a root of *P. gracilis bar* 40 µm. **b** *Paris*-type AM: hyphal coils in root cortex of *P. tenuisecta bar* 40 µm. *A* arbuscule, *HC* hyphal coil, *IH* intraradical hypha, *PS* penetration site

rootlets. It was previously suggested that parasitic plants do not form mycorrhizal associations, which is obviously not the case for *Pedicularis*. Coexistence of parasitic organs and AMF in the same rootlets suggests that being parasitic does not conflict with being mycorrhizal in *Pedicularis* species.

Unlike holoparasitic members of Orobanchaceae, seed germination of *Pedicularis* is independent of signals from host plants (Li et al. 2007), which may set their seedlings at a risk of high mortality due to lack of nutrient or water supply when host plants are not available. Considering the ubiquity of AMF, being mycorrhizal may help seedlings of *Pedicularis* to survive in case of the absence of proper host plants. Theoretically, *Pedicularis* plants without surrounding hosts may have higher mycorrhizal colonization levels than those attached to proper host plants. However, this hypothesis needs to be testified by further and more specific research.

The high colonization frequency and heavy colonization level by AMF indicate a significant ecological role of these fungi. Frequent detection of vesicles in examined species suggests a role of AMF in nutrient cycling of *Pedicularis*. Yet, the functional relations between the two nutrient strategies await more experimental studies.

According to previous findings, some *Pedicularis* species were considered obligate parasites, which would not survive without the presence of proper host plants (Piehl 1965; Lackney 1981; Petrů 2005), whereas others are facultative ones, which can grow well with or without a host plant (Sprague 1962; Nickrent 2002). Despite the difference in their dependence on host plants, all studied *Pedicularis* species were reported to have a very wide host range, which could reach up to 80 species from 35 families (Piehl 1963). Whether Chinese *Pedicularis* are facultative or not remains unclear. But, our preliminary studies on the host range of several Chinese species revealed that Chinese *Pedicularis* also have very wide host ranges (Li 2007). All the findings indicate that *Pedicularis* species are primitive parasitic plants, showing little host specificity and partial dependence on host plants. Lack of specificity in the parasitic mode may facilitate another strategy to develop or maintain (e.g., being mycorrhizal). According to Lackney (1981), *Pedicularis* may be parasitic due to an inability to obtain iron or phosphorus. Since most AMF can enhance nutrient (particularly phosphorus) uptake of host plants (Harley and Smith 1983; Aarle et al. 2002; Ryan et al. 2003), being mycorrhizal may be an alternative strategy for these plants.

Although indirect influence of mycorrhizal fungi on the growth of parasitic plants during coinfection of host plants has recently been noticed by some (Davies and Graves 1998; Salonen et al. 2000; Salonen et al. 2001), studies concerning the direct relations between parasitic plants and their symbiotic fungi are lacking and no efforts have ever been taken to investigate the nutrient contribution by the fungal partners. This is something to be done to testify the exact role of mycorrhizal fungi in nutrient acquisition by parasitic plants. Also, previous experiments have indicated that some parasitic plants would not be colonized by mycorrhizal fungi even with the presence of mycorrhizal inoculants in greenhouse or laboratory conditions (Davies and Graves 1998; Salonen et al. 2001; Gworgwor and Weber 2003). The mechanism of being able to develop mycorrhizal associations by some hemi-parasitic plants (such as *Pedicularis*) but not by others (e.g., *Rhinanthus minor*, Davies and Graves 1998) requires further investigation.

Acknowledgements The authors thank Prof. Andrew Smith of the University of Adelaide for his kindly encouragement and critical reading of an earlier version of the manuscript. We are grateful to Prof. Marinus J. A. Werger of Utrecht University for his comments that greatly improved the manuscript. We thank the anonymous reviewers for their instructive comments and valuable suggestions that improved this manuscript. All remaining errors are solely the responsibility of the authors. The research was supported by the National Natural Science Foundation of P. R. China (Grant 30670207) and “Western Light” Talent Training Program of Chinese Academy of Sciences for the first author.

References

Aarle IMV, Rouhier H, Saito M (2002) Phosphatase activities of arbuscular mycorrhizal intraradical and extraradical mycelium, and their relation to phosphorus availability. Mycol Res 106:1224–1229 doi:10.1017/S0953756202006470

Atsatt PR (1973) Parasitic flowering plants: how did they evolve? Am Nat 107:502–510 doi:10.1086/282853

Brundrett MC (2002) Coevolution of roots and mycorrhizas of land plants. New Phytol 154:275–304 doi:10.1046/j.1469-8137.2002.00397.x

Cameron DD, Seel WE (2007) Functional anatomy of haustoria formed by Rhinanthus minor: linking evidence from histology and isotope tracing. New Phytol 174:412–419 doi:10.1111/j.1469-8137.2007.02013.x

Cameron DD, Coats AM, Seel WE (2006) Differential resistance among host and non-host species underlies the variable success of the hemi-parasitic plant rhinanthus minor. Ann Bot (Lond) 98:1289–1299 doi:10.1093/aob/mcl218

Cavagnaro TR, Gao LL, Smith FA, Smith SE (2001) Morphology of arbuscular mycorrhizas is influenced by fungal identity. New Phytol 151:469–475 doi:10.1046/j.0028-646x.2001.00191.x

Chen ST, Guan KY (2001) Mycorrhizal study on four species of *Pedicularis*. Acta Bot Yunnanica 23(3):331–334 in Chinese

Cripps CL, Eddington LH (2005) Distribution of mycorrhizal types among alpine vascular plant families on the Beartooth Plateau, Rocky Mountains, USA, in reference to large-scale patterns in arctic-alpine habitats. Arct Alp Res 37:177–188 doi:10.1657/1523-0430(2005)037[0177:DOMTAA]2.0.CO;2

Davies DM, Graves JD (1998) Interactions between arbuscular mycorrhizal fungi and the hemiparasitic angiosperm *Rhinanthus minor* during co-infection of a host. New Phytol 139:555–563 doi:10.1046/j.1469-8137.1998.00211.x

Elias SI, Souza VC, Appezzato-da-gloria B (2001) Anatomical Confirmation of Root Parasitism in Brazilian *Agalinis* Raf. Species (Scrophulariaceae). Braz Arch Biol Tech 44:303–311

Estabrook EM, Yoder JI (1998) Plant-plant communications: rhizosphere signaling between parasitic angiosperms and their hosts. Plant Physiol 116:1–7 doi:10.1104/pp.116.1.1

Francis R, Read DJ (1984) Direct transfer of carbon between plants connected by vesicular- arbuscular mycorrhizal mycelium. Nature 307:53–56 doi:10.1038/307053a0

Gerdemann JW (1965) Vesicular-arbuscular mycorrhizas formed on maize and tulip tree by *Endogone fasciculata*. Mycologia 57:562–575 doi:10.2307/3756732

Gworgwor NA, Weber HC (2003) Arbuscular mycorrhizal fungi-parasite-host interaction for the control of *Striga hermonthica* (Del.) Benth. in sorghum. Mycorrhiza 13:277–281 *Sorghum bicolor* (L.) Moenchdoi:10.1007/s00572-003-0238-5

Harley JL, Harley EL (1987) A check-list of mycorrhiza in the British flora. New Phytol 105:1–102 doi:10.1111/j.1469-8137.1987.tb00674.x

Harley JL, Smith SE (1983) Mycorrhizal symbiosis, 1st edn. Academic, London

Heide-Jorgensen HS, Kuijt J (1995) The haustorium of the root parasite *Triphysarla* (Scrophulariaceae), with special reference to xylem bridge ultrastructure. Am J Bot 82(6):782–797 doi:10.2307/2445619

Khalid AN, Iqbal SH (1995) Mycotrophy in a vascular stem parasite *Cuscuta reflexa*. Mycorrhiza 6:69–71 doi:10.1007/s005720050109

Kohn LM, Stasovski E (1990) The mycorrhizal status of plants at Alexandra Fiord, Ellesmere Island, Canada, a high arctic site. Mycologia 82:23–35 doi:10.2307/3759959

Kubota M, McGonigle TP, Hyakumachi M (2005) Co-occurrence of *Arum*- and *Paris*-type morphologies of arbuscular mycorrhizae in cucumber and tomato. Mycorrhiza 15:73–77 doi:10.1007/s00572-004-0299-0

Lackney VK (1981) The parasitism of *Pedicularis lanceolata* Michx., a root hemiparasite. Bull Torrey Bot Club 108:422–429 doi:10.2307/2484442

Lesica PL, Antibus PK (1986) Mycorrhizal status of hemiparasitic vascular plants in Montana, U.S.A. Trans Br Mycol Soc 86: 341–343

Li HL (1951) Evolution in the flowers of *Pedicularis*. Evolution Int J Org Evolution 5:158–164 doi:10.2307/2405766

Li AR (2007) Studies on the limiting factors to the introduction and cultivation of several *Pedicularis* species from Yunnan Province, China. Doctoral thesis for Kunming Institute of Botany, Chinese Academy of Sciences. Kunming, P. R. China (in Chinese)

Li AR, Guan KY (2007) Mycorrhizal and dark septate endophytic fungi of *Pedicularis* species from northwest of Yunnan Province, China. Mycorrhiza 17:103–109 doi:10.1007/s00572-006-0081-6

Li AR, Guan KY, Probert RJ (2007) Effects of light, scarification and gibberellic acid on seed germination of eight *Pedicularis* species from Yunnan, China. HortScience 42 (5):1259–1262

Marler MJ, Zabinski CA, Callaway RM (1999) Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. Ecology 80:1180–1186

Marvier MA, Smith DL (1997) Conservation implications of host use for rare parasitic plants. Conserv Biol 11:839–848 doi:10.1046/j.1523-1739.1997.96223.x

Moora M, Zobel M (1996) Effect of arbuscular mycorrhiza on inter- and intraspecific competition of two grassland species. Oecologia 108:79–84 doi:10.1007/BF00333217

Nickrent DL (2002) Parasitic plants of the world. In: López-Sáez JA, Catalán P, Sáez L (eds) Parasitic plants of the Iberian Peninsula and Balearic Islands. Mundi-Prensa Libros, Madrid, pp 7–27

Petrů M (2005) Year-to-year oscillations in demography of the strictly biennial *Pedicularis sylvatica* and effects of experimental disturbances. Plant Ecol 181:289–298 doi:10.1007/s11258-005-7223-3

Phillips JM, Hayman DS (1970) Improved procedures for clearing roots and staining parasitic and vesicular–arbuscular mycorrhizal fungi for rapid assessment of infection. Trans Br Mycol Soc 55:157–160

Phoenix GK, Press MC (2005) Linking physiological traits to impacts on community structure and function: the role of root hemi-parasitic Orobanchaceae (ex-Scrophulariaceae). J Ecol 93:67–78 doi:10.1111/j.1365-2745.2004.00950.x

Piehl MA (1963) Mode of attachment, haustorium structure, and hosts of *Pedicularis canadensis*. Am J Bot 50:978–985 doi:10.2307/2439904

Piehl MA (1965) Studies of root parasitism in *Pedicularis lanceolata*. Mich Botanist 4:75–81

Press MC, Phoenix GK (2005) Impacts of parasitic plants on natural communities. New Phytol 166:737–751 doi:10.1111/j.1469-8137.2005.01358.x

Rümer S, Cameron DD, Wacker R, Hartung W, Jiang F (2007) An anatomical study of the haustoria of Rhinanthus minor attached to roots of different hosts. Flora 202:194–200

Ryan MH, McCully ME, Huang CX (2003) Location and quantification of phosphorus and other elements in fully hydrated, soil-grown arbuscular mycorrhizas: a cryo-analytical scanning electron microscopy study. New Phytol 160:429–441 doi:10.1046/j.1469-8137.2003.00884.x

Salonen V, Sa H, Puustinen S (2000) The interplay between *Pinus sylvestris*, its root hemiparasite, *Melampyrum pratense*, and ectomycorrhizal fungi: Influences on plant growth and reproduction. Ecoscience 7:195–200

Salonen V, Vestberg M, Vauhkonen M (2001) The effect of host mycorrhizal status on host plant–parasitic plant interactions. Mycorrhiza 11:95–100 doi:10.1007/s005720100104

Schneider MJ, Stermitz FR (1990) Uptake of host plant alkaloids by root parasitic *Pedicularis* species. Phytochemistry 29:1811–1814 doi:10.1016/0031-9422(90)85021-7

Seel WE, Parsons AN, Press MC (1993) Do inorganic solutes limit growth of the facultative hemiparasite *Rhinanthus minor* L. in the absence of a host? New Phytol 124:283–289 doi:10.1111/j.1469-8137.1993.tb03818.x

Simard SW, Perry DS, Jones MD, Myrold DD, Durall DM, Molina R (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. Nature 388:579–582 doi:10.1038/41557

Smith SE, Read DJ (1997) Mycorrhizal symbiosis, 2nd edn. Academic, London

Smith FA, Smith SE (1997) Structural diversity in (vesicular)-arbuscular mycorrhizal symbioses. New Phytol 137:373–388 doi:10.1046/j.1469-8137.1997.00848.x

Sprague EF (1962) Parasitism in *Pedicularis*. Madrono 16:192–200

Treu R, Laursen GA, Stephenson SL, Landolt JC, Densmore R (1996) Mycorrhizae from Denali National Park and Preserve, Alaska. Mycorrhiza 6:21–29 doi:10.1007/s005720050101

Tsoong PC (1963) Scrophulariaceae (Para II). In: Chien SS, Chun WY (eds) Flora reipublicae popularis sinicae. vol. 68. Science, Beijing, pp 1–378 (in Chinese)

Väre H, Vestberg M, Eurola S (1992) Mycorrhiza and root-associated fungi in Spitsbergen. Mycorrhiza 1:93–104 doi:10.1007/BF00203256

Walter LEF, Hartnett DC, Hetrick BAD, Schwab AP (1996) Interspecific nutrient transfer in a tallgrass prairie plant community. Am J Bot 83:180–184 doi:10.2307/2445936

Watkins NK, Fitter AH, Graves JD, Robinson D (1996) Carbon transfer between C3 and C4 plants linked by a common mycorrhizal network. quantified using stable carbon isotopes.

Soil Biol Biochem 28:471–477 doi:10.1016/0038-0717(95)00189-1

Weber HC (1987) Studies in cultivated parasitic Scrophulariaceae. II. Host parasite interactions. Flora 179:35–44

Yamato M (2004) Morphological types of arbuscular mycorrhizal fungi in roots of weeds on vacant land. Mycorrhiza 14:127–131 doi:10.1007/s00572-003-0246-5

Yang HP, Holmgren NH, Mill RR (1998) *Pedicularis* L. In: Wu ZY, Raven PH (eds) Flora of China, Vol.. vol. 18. Science, Beijing, pp 97–209

Yoder J (1997) A species-specific recognition system directs haustorium development in the parasitic plant *Triphysaria* (Scrophulariaceae). Planta 202:407–413 doi:10.1007/s004250050144