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Host Dependence and Preference of the Root Hemiparasite, *Pedicularis cephalantha* Franch. (Orobanchaceae)

Yong-Quan Ren · Kai-Yun Guan · Ai-Rong Li · Xiao-Jian Hu · Le Zhang

Abstract The interaction between parasitic plants and their hosts is an important topic in both agriculture and ecology. Little, however, is known about that of the hemiparasite *Pedicularis*. It is essential to understand the host dependence and preference of *Pedicularis* for successful cultivation of plants in this genus and for understanding the roles they play in natural communities. We tested the effects of two herbaceous host species (*Trifolium repens* and *Polypogon monspeliensis*) on the survival and growth performance of *Pedicularis cephalantha*. Five *P. cephalantha* seedlings and two host plants were planted in each pot. In the control, no host plants were planted (treatment 1). Host plants were planted in three combinations: only *T. repens* (treatment 2) or *P. monspeliensis* (treatment 3) or a mixture of both (treatment 4). The results showed that *P. cephalantha* performed better in the presence of host plants, and host plants are more essential to *P. cephalantha* for proper development than for survival. The grass host *P. monspeliensis* proved to be a better host plant for *P. cephalantha* than the legume host *T. repens*. The high dependence of *P. cephalantha* on host plants and its host preference were demonstrated in this study. This is the first report of the performance of Chinese *Pedicularis* species in cultivation throughout all life stages (from seeds to seeds).

Keywords Alpine plant · Haustorium · Host-parasite interaction · Host specificity · Propagation

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Y.-Q. Ren · K.-Y. Guan (✉) · A.-R. Li · X.-J. Hu · L. Zhang
Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650204, Yunnan,
People’s Republic of China
e-mail: guanky@mail.kib.ac.cn

Y.-Q. Ren · X.-J. Hu · L. Zhang
Graduate School, Chinese Academy of Sciences, Beijing 100039, People’s Republic of China

Introduction

Parasitic plants are common and important members in many plant communities, and 3,000–5,000 plants can parasitize other plants (Marvier and Smith 1997; Qasem 2006). Parasitic plants can be divided into holoparasites and hemiparasites based on their nutrient dependence on hosts. Hemiparasites contain chlorophyll and can photosynthesize, but still partially rely on their host plants as a source of water and nutrients through nodule-like structures called haustoria (Pate 2001; Wesselingh and van Groenendael 2005). The best-studied parasitic plant species are generally economically important parasites. However, compared with economically important parasitic plants, our understanding of most economically less important parasites is lacking, which is particularly the case with the knowledge of interaction between these parasites and their host plants. Accumulating evidence has shown that economically less important parasitic plants may play significant ecological roles that have been overlooked before (Joshi et al. 2000; Quested et al. 2003; Press and Phoenix 2005; Bardgett et al. 2006; Watson 2009), such as determining the structure of natural communities (Gibson and Watkinson 1992; Joshi et al. 2000; Pywell et al. 2004; Press and Phoenix 2005), enhancing the amelioration of physical stress conditions (Grewell 2008), and facilitating grassland restoration (Bullock and Pywell 2005; Watson 2009).

Pedicularis L. (Orobanchaceae) is a genus consisting of about 600 root hemiparasitic species worldwide, primarily distributed in mountainous areas of southwestern China, and widespread in frigid, alpine belts in the northern hemisphere (Yang et al. 1998). Plants of this genus have high pharmacological value (Guan et al. 2006) as well as potential ornamental value. Although *Pedicularis* species have long been known as root hemiparasitic plants, only a very limited number have been experimentally examined for their parasitic habit (Piehl 1963; Weber 1976, 1987; Lackney 1981). Little is known about the host requirements and the relative importance of particular host species for the hemiparasitic *Pedicularis*. The lack of such information represents a gap in our knowledge of the interaction between these parasitic plants and their hosts.

Of a few existing studies regarding the host range of *Pedicularis* species, conclusions about the host range of some *Pedicularis* species were made based on field observations, in which cases host plants were determined merely by the existence of haustoria (Piehl 1963; Weber 1976). Some root hemiparasites, however, have been found to be able to form haustorium-like structures on non-host plants (Cameron et al. 2006) or even on inorganic objects such as tiny pebbles (Piehl 1963). In most cases, such haustoria are poorly differentiated and have no actual function in nutrient acquisition (Cameron et al. 2006). Nevertheless, it is extremely difficult to tell the non-functional haustoria from functional ones without anatomic analysis or other more sophisticated examinations. Consequently, it is impossible to ascertain whether a host species upon which more haustoria are formed functions better than a host with less haustoria without further examination. In this regard, a host list compiled merely according to the existence of haustoria may be misleading as a basis for attempts at the cultivation of these hemiparasites (Marvier and Smith 1997). A relatively reliable method to test whether a species can function as host is to experimentally grow hemiparasites with it. Previous cultivation studies focusing on the interactions between *Pedicularis* and its host plants have not proven successful (Li and Guan 2008), which may account, at least partly, for the scarcity of documented reports on cultivation of *Pedicularis* species. As far as we know, the limited published investigations on cultivation of *Pedicularis* focus mainly on the performance of *Pedicularis* in its early stages, such as seed germination and seedling development (Lackney 1981; Li et al. 2007; Ren and Guan 2008). However, little is known about the host dependence and preference of *Pedicularis* species based on their whole life performance.

We designed the present study to understand host dependence and preference of one Chinese *Pedicularis* species based on the whole life performance of the parasitic species growing with different combinations of host species. We address the following specific questions: *i*) Does performance of this hemiparasite depend on host availability? *ii*) Does performance of this hemiparasite vary with different hosts or host combinations? A better understanding of host effects is essential for developing effective measures to cultivate *Pedicularis* species successfully. Answers to these questions are necessary to understand the ecological roles the genus *Pedicularis* plays in natural communities.

Material and Methods

Pedicularis cephalantha Franch., the target parasitic species in the present study, is a herbaceous perennial endemic to Northwestern Yunnan, China, and widespread in alpine meadows, 12–20 cm in height and with subcapitate inflorescences bearing red flowers. Hemiparasites with large host plants suffer consequences of competition with their own host (Calladine et al. 2000). As *P. cephalantha* are low herbaceous plants in open habitats, we preferred to select low herbaceous hosts to avoid the potential competitive influence. Herbaceous hosts are generally categorized into three functional groups: grasses, legumes and forbs (Jiang et al. 2008). Forbs generally represent the worst hosts for parasitic plants because they can employ some defense mechanisms to prevent the abstraction of solutes in these host plants (Cameron et al. 2006; Cameron and Seel 2007). Grasses are generally considered to be good hosts because the finely branched architecture of grass roots may greatly increase the likelihood of contact between the parasite and the host (Gibson and Watkinson 1989; Marvier and Smith 1997). N-fixing legumes serve as ideal host plants for some root hemiparasites (Tennakoon and Pate 1996; Radomiljac et al. 1999; Cameron et al. 2006). Furthermore, field surveys of natural habitats of some Chinese *Pedicularis* species indicate that these hemiparasites may have close associations with grasses and legumes (Ren et al., unpubl. data). Therefore, in the present study, we selected one representative of each of these two groups as hosts. As a host in cultivation, the plant species must adapt to the local climate and be easy to grow. Thus, we selected *Polypogon monspeliensis* (L.) Desf. and *Trifolium repens* L., both of which are widespread in Kunming, China, to test their effects on growth performance of *P. cephalantha*.

The experiment was conducted in a nursery bed equipped with an auto-irrigation spray appliance in the Kunming Botanical Garden (25°01′ N, 102°41′ E, altitude: 1,990 m). The nursery bed was 50 cm above ground to avoid root contamination between treatments. *P. cephalantha* were planted in 9-inch earthenware pots filled with humus soil. Five *P. cephalantha* seedlings and two host plants were planted in each pot. In the control, no host plants were planted (treatment 1). Host plants were planted in three combinations: only *T. repens* (treatment 2) or *P. monspeliensis* (treatment 3) or a mixture of both (treatment 4). For each treatment, there were five replicates with one exception of six replicates in treatment 2. For each replicate, there were eight pots. Four pots were arranged in a line on the nursery bed, and a replicate consisted of eight pots (two lines). All replicates were arranged randomly. Altogether 168 pots were used in this study.

Seeds of *P. cephalantha* were collected in October 2007 from Shangri-La, Yunnan (27°45′ N, 99°46′ E, altitude: 3,370 m). Seeds were dried under ambient conditions and then stored in paper envelopes at 4°C until the initiation of experiments. *T. repens* and *P. monspeliensis* seeds were collected in the Kunming Botanical Garden in September 2007 and late March 2008, respectively. These seeds were stored in paper envelopes under ambient conditions until the experiment commenced. Based on the results of Ren and Guan (2008), the seeds of *P. cephalantha* were imbibed for 24 h with 500 ppm GA_3 at 25°C in darkness on 1st April 2008. After treatment, seeds were cultured in 9-cm Petri dishes with two layers of filter paper saturated with distilled water. Whenever needed to keep the filter paper moist, additional water was added. Petri dishes were placed in a growth chamber at 10/20°C alternating temperature (12 h : 12 h), with fluorescent lamp light during the period at a higher temperature.

On 1 April 2008, seeds of hosts were sown in the pots, and enough host seedlings were available 10 days later. Before transplanting *P. cephalantha* seedlings, redundant host seedlings were removed, leaving only two according to the treatment arrangement. On 20 April, five germinated seeds of *P. cephalantha* were transplanted into each pot (radicle was approximately 5–10 mm long). On 27 April, most *P. cephalantha* seedlings emerged. The quantity of seedlings in each pot was recorded. From then on, the survival quantity of *P. cephalantha* seedlings was recorded weekly. To reduce competition from hosts, most leaves and stems of both host plants in all host treatments were cut down to about 4 cm above soil level on 10 June for the first time. From then on, the practice of host defoliation was repeated every two weeks. To protect the plants from pests, we sprayed pesticide weekly. All pots were watered whenever needed to avoid water stress during the whole growing season.

Harvesting commenced on 19 August, about 4 months after the hemiparasite and hosts were planted together. At this time, some *P. cephalantha* plants were fruiting. The growth parameters of *P. cephalantha* in each pot measured were as follows: plant height, length of the longest leaf, and quantity of flowering plants. Four pots (one line) from each replicate were selected to measure root and shoot dry weight. Roots of *P. cephalantha* were washed carefully to reduce the damage to rootlets, and then bagged and oven-dried at 80°C for 48 h before weighing with an electronic balance. The remaining four pots in the other line from each replicate were left for examinations of haustorial quantity and size. In each treatment, we selected pots with only one *P. cephalantha*, to test the quantity and size of haustoria attached to hosts. The soil was loosened by soaking for 24 h in water, to reduce the risk of damaging haustorial connections (Gibson and Watkinson 1989; Kenji et al. 2008).

Successive washing progressively removed soil from the entangled root systems of parasite and hosts, with haustorial connections to the host root mostly intact. The value of haustorial diameter was used in haustorial size measurement, and we used vernier caliper to measure diameter.

The survival rates of *P. cephalantha* were calculated from the quantities of living plants at the time of harvest. The survival and flowering rates of *P. cephalantha* used in analysis were obtained from the total of eight pots in each replicate. For length of the longest leaf and height of plant, mean values of eight pots were used in analysis, while for dry weight data, values of four pots from each replicate were used. Rate data were arcsine-transformed, dry weight data were log-transformed, and data of height and length were square root-transformed before analysis. The data were analyzed by ANOVA and SNK test. No self-attached haustorium was observed from the control (treatment 1), and haustoria were obtained only from eight pots in the other three host treatments (2–3 pots per treatment). Flowering rate of *P. cephalantha* was zero in the control (treatment 1). To avoid violating the homoscedasticity assumption, differences in flowering rate, haustorial quantity and size among three host treatments were analyzed using one-way ANOVA and SNK test. Data for haustorial quantity were log-transformed before analysis. All statistical analyses were performed using SPSS statistical software (SPSS 13.0 for Windows).

Results

At the time of harvest, the life stages of *Pedicularis cephalantha* plants varied in different treatments and even within the same treatment. According to the criteria of Petrů (2005), some *Pedicularis* plants grown with hosts matured, whereas all *Pedicularis* in the control treatment (grown without any host) were still in the juvenile stage (Fig. 1a). At harvest, most matured *Pedicularis* plants were at fruiting stage and some mature seeds were obtained. The developmental stage of *P. cephalantha* varied even in the same treatment, and some plants grown with hosts were still in the juvenile stage. Figure 1b shows the different life stages of *P. cephalantha* at the time of harvest.

Except for flowering rate, survival rate and root-shoot ratio did not depend on host presence and host combinations. In all treatments, survival rates decreased over time, the highest survival curve was obtained from *P. cephalantha* grown with a mixture of both hosts and the lowest one was obtained from that grown without any host (Fig. 2). However, there was no significant difference on survival rates between treatments (F=1.267, P=0.317) (Fig. 3). In the control treatment, *P. cephalantha* grown independently, the lowest value of root-shoot ratio was obtained, while the difference between treatments was also not significant (F=2.025, P=0.149) (Fig. 3). Flowering rate depended strongly on host presence, and no *Pedicularis* flowered in the control treatment, but the difference was not significant between the three host combinations (F=3.680, P=0.054) (Fig. 3).

All growth parameters of *P. cephalantha* depended strongly on host presence and host combinations (Fig. 3). All growth parameters of *P. cephalantha* grown with hosts were better than that of the control treatment, and all growth parameters varied significantly among host combinations. Growth parameters of *P. cephalantha* grown

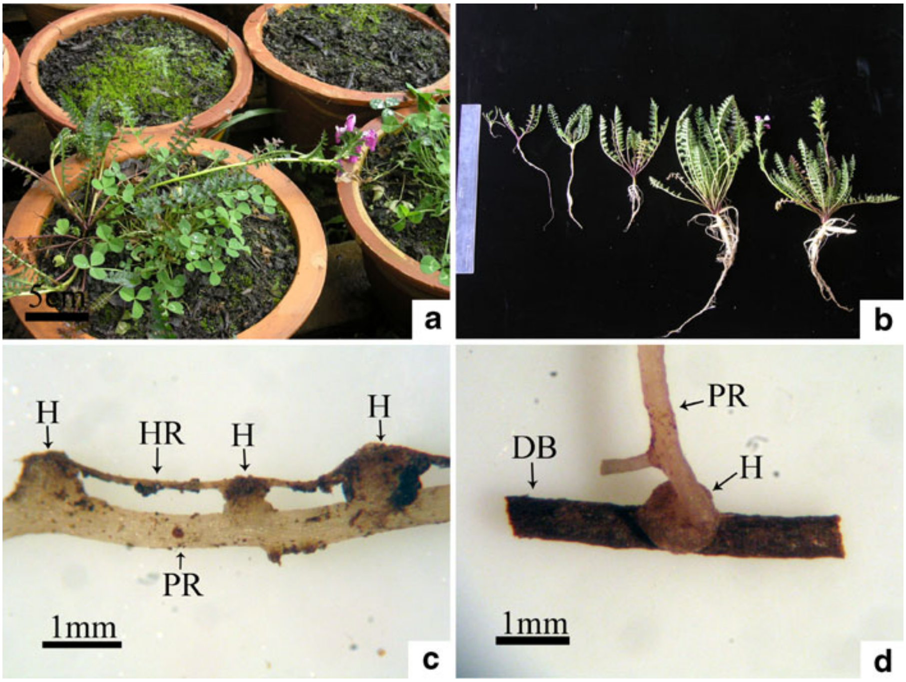
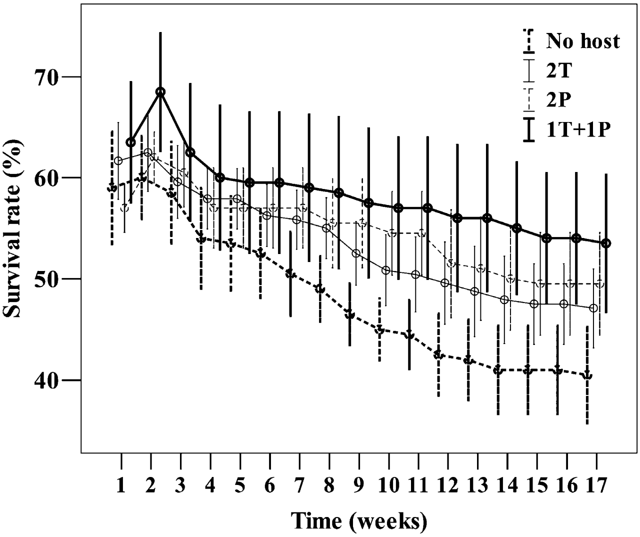


Fig. 1 Growth performance of *Pedicularis cephalantha* and haustoria formed. **a** Host dependence of *P. cephalantha*. The bottom left pot shows a flowering plant grown with host plants, the upper pots show *P. cephalantha* grown in the absence of host being still in the juvenile stage or dead. **b** Different life stages of *P. cephalantha* four months after transplanting; rule – 30 cm. **c** Haustoria formed on a rootlet of *Polypogon monspeliensis*; H – haustorium, HR – host root, PR – *Pedicularis* root. **d** A haustorium-like structure formed on a tiny dead branch; H – haustorium, DB – dead branch, PR – *Pedicularis* root

Fig. 2 Survival rate curves of *Pedicularis cephalantha* from different treatments. The hemiparasite was grown without host (No host), with two individuals of the legume *Trifolium repens* (2T), with two individuals of the grass *Polypogon monspeliensis* (2P), and with one individual each of *T. repens* and *P. monspeliensis* (1T + 1P). Vertical bars denote 1SE



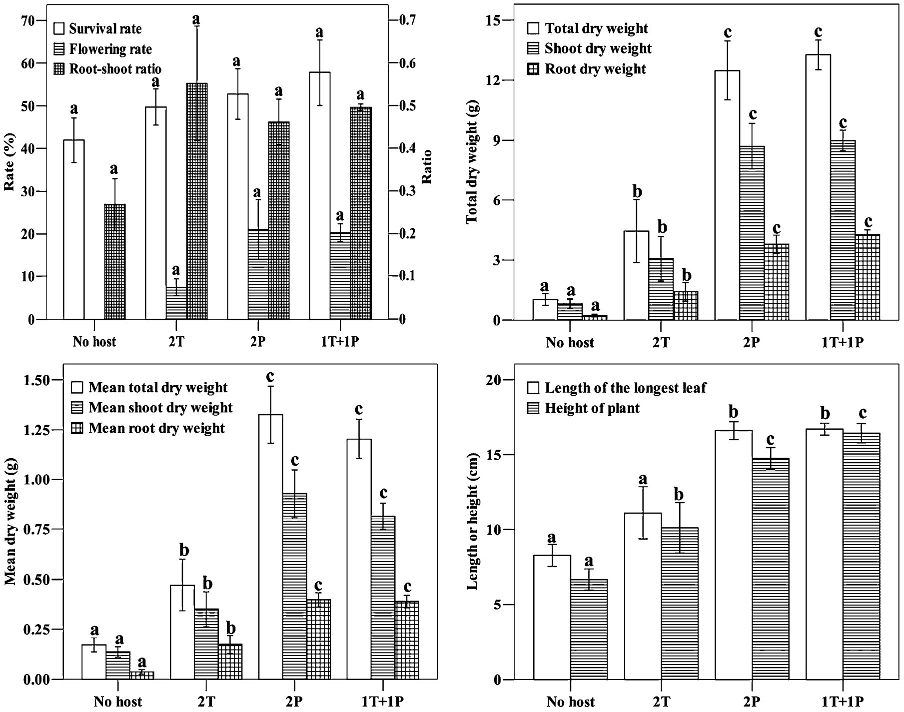


Fig. 3 Growth parameters of *Pedicularis cephalantha* in different treatments. The hemiparasite was grown without host (No host), with two individuals of the legume *Trifolium repens* (2T), with two individuals of the grass *Polypogon monspeliensis* (2P), and with one individual each of *T. repens* and *P. monspeliensis* (1T + 1P). Vertical bars denote 1SE, and different letters represent significant different treatment means by SNK test at 5% level of significance

with *Polypogon monspeliensis* were better than that grown with *Trifolium repens*. In particular, for all growth parameters of *P. cephalantha*, the highest values were obtained from plants grown with grass hosts of *P. monspeliensis* or the mixture of both hosts. The highest values of total dry weight (DW), total shoot DW and total root DW, length of the longest leaf, height of plants, and flowering rate were all obtained from *P. cephalantha* grown with the mixture of both hosts. The highest values of mean plant DW, mean plant shoot DW and mean plant root DW were all obtained from *P. cephalantha* grown with grass hosts of *P. monspeliensis*. All these parameters were significantly different ($P<0.01$) between treatments. Although almost all the best growth parameters of *P. cephalantha* were obtained from the treatment with a mixture of both hosts, all these parameters were not significantly different from that of the treatment with grass hosts of *P. monspeliensis* alone (Fig. 3).

Neither *P. monspeliensis* nor *T. repens* had a significant effect on both survival rate and root-shoot ratio of *P. cephalantha* by two-factor ANOVAs (Table 1). However, two-factor ANOVAs indicated that host plants had significantly positive effects on most other growth parameters. Of the two host species studied, *P. monspeliensis* had much greater positive effects on growth of *P. cephalantha* than *T. repens* (Table 1), with extremely significant effects ($P<0.001$) on flowering rate, height, longest leaf length and all dry weight parameters four months after

Table 1 Analysis of variance of final *Pedicularis cephalantha* survival and growth parameters four months after *P. cephalantha* plants were planted together with hosts *Trifolium repens* (T) and *Polypogon monspeliensis* (P)

Source of variation	T			P			T*P			Error	
	d.f.	MS	*F*	d.f.	MS	*F*	d.f.	MS	*F*	d.f.	MS
Flowering rate	1	58.067	0.850	1	1494.801	21.876***	1	85.859	1.257	17	68.331
Survival rate	1	215.220	1.236	1	464.490	2.668	1	10.033	0.058	17	174.113
Height of plants	1	0.792	4.994*	1	6.295	39.699***	1	0.159	1.001	17	0.159
Length of the longest leaf	1	0.243	1.709	1	5.290	37.148***	1	0.216	1.520	17	0.142
Total dry weight (DW)	1	0.225	8.719**	1	2.251	87.263***	1	0.158	6.122*	17	0.026
Total shoot DW	1	0.139	5.949*	1	1.826	78.211***	1	0.103	4.422	17	0.023
Total root DW	1	0.130	9.995**	1	1.208	92.773***	1	0.060	4.578*	17	0.013
Mean total DW	1	0.007	1.877	1	0.296	84.018***	1	0.017	4.872*	17	0.004
Mean shoot DW	1	0.003	1.226	1	0.168	69.429***	1	0.012	4.968*	17	0.002
Mean root DW	1	0.003	4.119	1	0.054	68.882***	1	0.004	5.008*	17	0.001
Root-shoot ratio	1	1329.306	3.358	1	251.033	0.634	1	814.005	2.056	17	395.849

* – $P<0.05$, ** – $P<0.01$, *** – $P<0.001$. Rate/ratio data were arcsine-transformed, dry weight data were log-transformed, and data of height and length were square root-transformed before analysis.

P. cephalantha and hosts were planted together, while *T. repens* had significant effects only on height, total shoot DW ($P<0.05$), total DW and total root DW ($P<0.01$).

In all host treatments, *Pedicularis* plants formed haustoria on the root of host plants (Fig. 1c). In the control, virtually no haustorium was observed except a haustorium-like structure detected attached to a tiny dead branch in the substrate of humus soil (Fig. 1d). The highest value of haustorium quantity was obtained from *P. cephalantha* grown with two plants of *P. monspeliensis*, and the lowest value was obtained from those grown with two plants of *T. repens*. The difference in haustorium quantities among different parasite-host combinations was not significant ($P=0.093$). Nevertheless, size of haustorium was significantly different in different treatments ($P=0.034$), and the largest size was obtained from *P. cephalantha* grown with *T. repens* (Table 2).

Discussion

The performance of *Pedicularis cephalantha* in the absence/presence of potential hosts was examined in pot cultivation. In agreement with several previous studies on root hemiparasitic species (Lackney 1981; Radomiljac et al. 1998; Matthies and Egli 1999; Puustinen and Salonen 1999; Loveys et al. 2002), we found that the presence of host plants favored the performance of *P. cephalantha*. Studies on potted

Table 2 Quantity and size of haustoria between one *Pedicularis cephalantha* individual and two hosts

Hosts	2T	2P	1T + 1P	d.f.	MS	*F*	*P*
Haustorial quantity	35.25±22.65a	139.50±79.90a	79.90±31.11a	2	0.297	3.972	0.093
Haustorial size (mm)	0.88±0.08b	0.73±0.07ab	0.62±0.10a	2	0.046	7.173	0.034

Data are means and standard deviations, different letters represent significant different treatment means by SNK test at 5% level of significance. The hemiparasite was grown with two individuals of *Trifolium repens* (2T), with two individuals of *Polypogon monspeliensis* (2P), and with one individual each of *T. repens* and *P. monspeliensis* (1T + 1P). Data for haustorial quantity were log-transformed before analysis.

seedlings showed that *P. cephalantha* can survive for up to four months without any host, indicating no obligate requirement for host species to survive as juveniles. However, in the absence of hosts, all *P. cephalantha* plants were trapped in the juvenile stage even after four months' growth, when they otherwise would be in the reproductive phase, which means that host plants are essential to *P. cephalantha* not for survival but for proper development. With the presence of hosts, we successfully obtained seeds from seeds in the cultivation of *Pedicularis* species.

Different host species have different effects on the growth performance of parasites and parasites achieve optimal performance only when attached to a suitable host (Lackney 1981; Calladine et al. 2000; Cameron et al. 2006; Jiang et al. 2007). *Polypogon monspeliensis* showed much greater effects on promoting the growth of *P. cephalantha* than *Trifolium repens* in the present study. According to previous research, root hemiparasitic plants generally have less host specificity and may exploit multiple hosts simultaneously to benefit from different nutritional contributions (Marvier and Smith 1997; Marvier 1998). The treatment with the mixture of two hosts showed the highest survival rate and the best overall growth performance.

The present study shows that *P. monspeliensis* is a good host. A similar observation has been made by a prior field study (Gawler et al. 1987), which found that *Pedicularis furbishiae* seedlings survived better under graminoid-dominated vegetation than under forb-dominated. In a cultivation experiment, Matthies and Egli (1999) demonstrated that the grass *Lolium perenne* was a far better host than the legume *Medicago sativa* for the hemiparasite *Rhinanthus alectorolophus*. The probability of contacting and successfully attacking a host is a main factor involved in determining host suitability (Marvier and Smith 1997), and grass hosts have a high contact rate and thus likelihood of a successful parasite attack (Gibson and Watkinson 1989). *P. monspeliensis* has highly branched and thin roots, and can therefore be a particularly good host in this study. The highest quantity of haustoria was obtained from *P. cephalantha* grown with *P. monspeliensis*, and the performance of *P. cephalantha* grown with *P. monspeliensis* was almost as good as that grown with the mixture of both hosts.

Being a legume species, *T. repens* was expected to be the best host for *P. cephalantha*. However, *T. repens* in treatment 2 was proved to be the "worst host". Unlike *P. monspeliensis*, *T. repens* has less fibrous rootlets and less surface area and thus a reduced likelihood of being attacked by haustoria of *P. cephalantha*. Poor growth of *Cuscuta subinclusa* on a legume host *Lotus scoparius* was previously suggested to be due to fewer haustorial connections (Kelly 1990). Similarly, in this study, fewer haustorial connections were formed on *T. repens* than on

P. monspeliensis. *T. repens* grew quickly and often shaded seedlings of *P. cephalantha*. Thus, *P. cephalantha* had to compete with its host instead of deriving benefits from it, or the benefit was cancelled out by competition. According to Matthies (1995), host-parasite relationships may also include competitive interaction. The bad performance of *P. cephalantha* in this treatment may be due in part to competition from hosts. Well developed haustoria and a less defensive response of the host, rather than the ability to fix nitrogen, may be the primary factors influencing the performance of hemiparasite (Jiang et al. 2008). Taking these factors of fewer haustorial connections and strong competition into account, *T. repens* is not necessarily as good a host as expected. This result is consistent with the findings of Radomiljac (1998), who reported that legumes are not necessarily better hosts than non legumes for *Santalum album*.

Although the simple comparison between two hosts in the present study does not allow a general conclusion concerning host quality, it seems that the root architecture of hosts is an important factor involved in determining host suitability. Host preference provides a mechanism by which the parasites can selectively parasitize components of the natural community in which they occur and then can affect the community structure (Gibson and Watkinson 1989, 1992; Pywell et al. 2004). It this study, we found that *P. cephalantha* benefit more from *P. monspeliensis* than *T. repens*. Although the effects of *P. cephalantha* on host performance are not addressed in this study, the host preference of *P. cephalantha* can be an important guideline for the cultivation of this genus as well as other research in ecology.

Parasites have been reported to suffer reduced survival rates as a result of competition with their host (Keith et al. 2004; Ahonen et al. 2006). To reduce competition from hosts, host defoliation was conducted in the present study. However, relative host suitability to a hemiparasite can change with defoliation (Puustinen and Salonen 1999). Effects of defoliation may vary among hosts, because the manner in which hosts suffer from defoliation may be significantly different. Thus, results of this study should be interpreted carefully in comparing host quality. Further experiments including a gradient of defoliation would be necessary to determine the relative importance of different host species.

In this experiment, *P. cephalantha* plants had root-shoot ratios between 0.26 and 0.50, which are similar to the ratios (between 0.29 and 0.34) of the hemiparasite *Santalum album* (Radomiljac et al. 1998). Jiang et al. (2007) obtained lower root-shoot ratios (0.043–0.23) with the hemiparasite *Rhinanthus minor*. These are low ratios compared to the overall result (6.3 for mean value and 5.7 for median value) of Yang et al. (2010) based on a large-scale survey on China's grasslands plants in 265 sites. Seedlings grown independently in treatment 1 were the smallest plants and had the lowest root-shoot ratios. In the early life stage, *P. cephalantha* establishes a large shoot at the expense of its own root system. This may be an adaptation to increase its ability of photosynthesis, which maximizes plant growth by giving priority to shoot growth over root growth. The relatively small root reduces nutrient and water uptake, and thus a lower root-shoot ratio may lead to a higher mortality rate of *P. cephalantha*. However, maybe this represents a strategy for the hemiparasite that does not depend so much on its own root system. Hemiparasite rely on its host to avoid water and mineral deficiencies (Glatzel and Geils 2009), and to obtain part of its carbon nutrition (Logan et al. 2002).

This study clearly demonstrates that the presence of suitable hosts improves the growth performance of *P. cephalantha*. The results of this study support the hypothesis that hemiparasites depend on hosts and may respond differently to different hosts. The host preference of *Pedicularis* species indicates that they may influence the structure of natural communities by modifying the competitive relationships between the component host species. The large differences in *P. cephalantha* growth performance when grown with different host arrangements in this study highlight the importance of identifying suitable hosts or host combinations to promote the cultivation of the genus of *Pedicularis*.

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