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Host Range and Selectivity of the Hemiparasitic Plant *Thesium chinense* (Santalaceae)

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- *Background and Aims Thesium chinense* is a hemiparasitic plant that is common in grassland habitats of eastern Asia. Although the physiology of *Thesium* has been well studied in attempts to control its weedy habit, there have been few ecological investigations of its parasitic life history. *Thesium chinense* is thought to parasitize species of Poaceae, but evidence remains circumstantial.
- *Methods* A vegetation survey was conducted to test whether any plant species occurs significantly more often in plots with *T. chinense* than expected. In addition, haustorial connections were examined directly by excavating the roots and post-attachment host selectivity was evaluated by comparing the observed numbers of haustoria on different hosts against those expected according to the relative below-ground biomass. Haustorium sizes were also compared among host species.
- *Key Results* Only two of the 38 species recorded, *Lespedeza juncea* and *Eragrostis curvula*, occurred more often in plots with *Thesium* than expected. In contrast to this, *T. chinense* parasitized 22 plant species in 11 families, corresponding to 57·9 % of plant species found at the study site. Haustoria were non-randomly distributed among host species, suggesting that there is some post-attachment host selectivity. *Thesium chinense* generally preferred the Poaceae, although haustoria formed on the Fabaceae were larger than those on other hosts.
- *Conclusions* This is the first quantitative investigation of the host range and selectivity of hemiparasitic plants of the Santalales. The preference for Fabaceae as hosts may be linked to the greater nutrient availability in these nitrogen-fixing plants.

Key words: Haustorium, hemiparasite, host range, host selectivity, Santalaceae, *Thesium chinense*.

INTRODUCTION

Around 1 % of angiosperm species have evolved to abstract resources from other plants in the form of root parasitism (Press and Graves, 1995). Compared with stem parasites that grow upon other plants above ground, identifying the hosts of root parasites is not straightforward in the field (Piehl, 1963; Musselman and Mann, 1977; Gibson and Watkinson, 1989). The Santalales is primarily composed of hemi- and holoparasitic plants that have a variety of life forms. However, apart from stem parasites in the Viscaceae, Loranthaceae and Misodendraceae, host associations in the remaining root parasites are little understood.

Thesium (Santalaceae) is a genus of herbaceous and woody root hemiparasites that are widely distributed in temperate and tropical regions of the Old World (Pilger, 1935). Some species are well-known agricultural weeds. The physiology of *Thesium* has thus been studied in an agronomic context; for example, mannitol metabolism of *Thesium* has been particularly well studied for the purpose of controlling its weedy habit (Fer *et al.*, 1993; Simier *et al.*, 1993, 1994, 1998; Williamson *et al.*, 2002). However, very little is known about its host range and selectivity in wild populations. For example, *Thesium chinense* is thought to parasitize species of Poaceae (Numata and Yoshizawa, 1975), but information is based on a limited number of observations and circumstantial evidence that these plants usually occur near plants from the family Poaceae. The situation is more or less the same in other members of *Thesium*, but the genus as a whole seems to be capable of using a wide range of angiosperms, including *Themeda* and *Poa* (Poaceae; Scarlett *et al.*, 2003), *Galium* (Rubiaceae; Renaudin *et al.*, 1981), barley and onion (Abu-Irmaileh, 1980) and grape (Dasgupta, 1988). Therefore, it is possible that each *Thesium* species parasitizes several host species within a population while having some preference for particular groups of hosts (e.g. Poaceae). Hence, it is necessary to examine root associations between *Thesium* and potential host plants in a given population and to quantify the strength of parasitism in order to understand the host range and post-attachment selectivity of *Thesium*. Knowledge of the parasitic life history not only provides basic biological information, but also contributes to a better understanding of how plants of the Santalales have evolved the current diversity of parasitic life forms.

The host range and selectivity of the root hemiparasite *T. chinense* were examined in a wild population situated on a riverside in central Japan. First, a vegetation survey was conducted to determine whether *Thesium* plants are significantly more likely to occur in association with particular plant species. Plants of *Thesium* as well as other root parasites take up host resources through a nodule-like structure called a haustorium. The abundance of haustoria

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in roots of all potential hosts was therefore directly examined and quantified and the host range and selectivity of *T. chinense* determined. This is the first quantitative analysis of host range and selectivity in root hemiparasitic plants of Santalales.

MATERIALS AND METHODS

Study plant

Thesium chinense (Santalaceae) is a perennial herb (Fig. 1) that is usually erect, but occasionally prostrate, and has branched stems up to 60 cm in length. The plant commonly occurs in disturbed habitats such as grasslands or riversides and quickly regenerates after fire. It has narrow, linear leaves, and the flowers are cylindrical, greenish-white, and approx. 2 mm long. *Thesium chinense*, in common with other root and stem parasites, takes up water and nutrients from its host by means of a specialized structure known as a haustorium (Fig. 1), which provides a physical as well as physiological bridge between parasite and host (Kuijt, 1969). The haustorium constitutes a hyaline body (the structure rich in nuclei involved in resource translocation and processing; Riopel and Timko, 1995), a penetration peg (the projection that enters host tissue; Tennakoon and Cameron, 2006) and a xylem element (the channel of nutrients and water to be absorbed from the host). Field studies were conducted by the riverside of the Kizu River, Kyoto Prefecture, Japan, during November and December 2007. During the study, *T. chinense* was mostly fruiting, but some plants were still in flower.

Association analysis

In order to determine if any plant species are more likely than others to grow in close proximity to *T. chinense*, a line transect vegetation survey was conducted. A 50-m transect was randomly placed within the riverside vegetation and 30×30 cm^2 quadrats established every 5 m, resulting in 11 quadrats per transect. This procedure was repeated for 19 transects for a total of 209 quadrats. A preliminary investigation indicated that the roots of *T. chinense* do not normally spread beyond 30 cm from the shoot; thus, the size of the quadrats was appropriate for inferring host–parasite associations. All plant species that occurred in each quadrat were recorded and a test was carried out to see if any species was more or less likely to occur in quadrats with *T. chinense* (Chuang and Heckard, 1971; Hodgson, 1973). The significance of species associations was assessed using Fisher's exact test. To avoid committing a type II error by testing small-sized samples, only species that occurred in >20 quadrats (the eight most-dominant species in the study site) were tested for association with *T. chinense*.

Examination of haustorial connections

The above association analysis is useful to determine if *T. chinense* is likely to occur in patches with particular plants at the population level. However, it is necessary to directly examine haustorial connections in order to correctly identify the host range. In addition, the host selectivity of *T. chinense* can be investigated by comparing the number of haustoria formed on the roots of each host species to that expected from the relative below-ground biomass of hosts

FIG. 1. (A) Riverside vegetation with *Thesium chinense*. Tc, *Thesium chinense*; Ac, *Artemisia capillaris*; Ec, *Eragrostis curvula*; Gv, *Galium verum*. (B) *Thesium chinense* and its host (*Artemisia princeps*). (C) Root of *T. chinense* (white) entangled in the root of its host (*Artemisia capillaris*; dark brown). (D) Haustorial connection of *T. chinense* and host (*Eragrostis curvula*) roots. Scale bar = 1 mm.

(Gibson and Watkinson, 1989). Note that the host selectivity in this case more likely reflects the suitability of host after infection (post-attachment selectivity) and does not necessarily indicate the degree to which *T. chinense* actively chooses among potentially available hosts prior to infection. To examine haustorial connections for the above purposes, nine samples of 30 × 30 × 20 (depth) cm^3 turf containing two to three *T. chinense* plants were randomly collected. Turf samples were taken to the laboratory, and the soil was loosened for 24 h in a waterbath; this reduced the risk of damaging haustorial connections when removing the soil and examining haustorial connections. The rhizobial nodules of legumes were easily distinguished from haustoria by their colour and shape. The host species was determined by tracing the root back to the shoot. After counting the number of haustoria formed on each host, the roots were oven-dried at 50 °C for 48 h and weighed to the nearest 0·01 g to calculate the relative below-ground biomass of each species. This was multiplied by the total number of haustoria found in the turf samples in order to obtain the expected distribution of haustoria across all of the potential hosts. The host selectivity of *T. chinense* was then tested using a χ^2 test. All nine turf samples were combined for the analysis.

Haustorium size

Host selectivity is likely to be reflected in the number of haustorial connections, but the results of such an analysis should be interpreted cautiously if the size of haustoria differs among host species. Therefore all haustoria were classified into six size categories: <1 mm, 1–1·5 mm, 1·5–2·0 mm, 2·0–2·5 mm, 2·5–3·0 mm and 3·0–3·5 mm. Differences in haustorium size among taxa were tested using the Kruskal–Wallis test, and *post hoc* multiple tests of pairwise differences were done using Scheffe's test.

RESULTS

Association analysis

A total of 38 plant species were identified in the 209 plots surveyed. Of these, only *Lespedeza juncea* ($P < 0{\cdot}01$) and *Eragrostis curvula* ($P < 0{\cdot}05$) had significantly positive associations with *T. chinense. Diodia teres* ($P < 0{\cdot}05$) had a significantly negative association with *T. chinense* (Table 1).

Examination of haustorial connections

The direct examination of haustorial connections revealed 22 species belonging to 11 families as hosts of *T. chinense* (Table 1; including four species that were found associated with *T. chinense* in preliminary observations: *Artemisia princeps*, *Diodia teres*, *Sporobolus fertilis* and *Sedum bulbiferum*). The observed and expected numbers of haustoria were significantly different (χ^2 test, $P < 0{\cdot}0001$; Table 2), suggesting that there is post-attachment selectivity. Significant differences were also found when data were analysed according to host plant families ($P < 0{\cdot}0001$; Table 3). Based on χ^2 values, *Andropogon virginicus* was a highly preferred host, whereas *Dianthus superbus* and *Potentilla chinensis* were less preferred (Table 2). In the same manner, Poaceae was highly preferred, whereas Caryophyllaceae and Rosaceae were hardly parasitized (Table 3). However, it should be noted that the observed/expected numbers of haustoria were too small in some species/families to confidently infer the significance of preference.

Haustorium size

The majority of haustoria were <1 mm in most of the species examined. However, the haustorium size differed significantly among species (Kruskal–Wallis test, $P < 0{\cdot}0001$; Table 4). The haustoria formed on *Lespedeza juncea* were significantly larger than those formed on *Andropogon virginicus*, *Cymbopogon tortilis*, *Eragrostis curvula*, *Agrostis* sp., *Rumex acetosella* and *Dianthus superbus* (Scheffe's test, $P < 0{\cdot}05$). In addition, *Pueraria lobata* had significantly larger haustoria than did *Rumex acetosella.* Similarly, the size of haustoria in Fabaceae was significantly larger than that in other families, expect Rosaceae and Oxalidaceae. Asteraceae had significantly larger haustoria than did Polygonaceae.

DISCUSSION

For many root parasites, host range and selectivity in wild populations are poorly known and little studied because this requires a careful and extensive excavation of the root. Consequently, studies have concentrated on examination of parasite performance in pots with different host species as an alternative to excavation study (Malcom, 1966). However, pot-based studies are not suitable for a full understanding of host range and may yield misleading predictions regarding the pattern of host use in the wild (Marvier and Smith, 1997). Therefore, the present study was undertaken in order to explore the pattern of host association in *T. chinense* in a wild population. This is the first quantitative analysis of host associations in root hemiparasitic plants of Santalales.

The association analysis indicated that the majority of plants in the study population had neither positive nor negative associations with *T. chinense*. However, it should be noted that the sample sizes were too small for most species to make meaningful comparisons (Table 1), and it is possible that there is a hidden preference that it was not possible to detect. Among the eight species tested for significance, *Lespedeza juncea* and *Eragrostis curvula* occurred significantly more often in plots with *T. chinense*. There was also a significant negative association between *Diodia teres* and *T. chinense*, but direct examination of the roots indicated that *Diodia teres* is in fact parasitized, suggesting that our indirect method does not correctly reflect the actual patterns of host–parasite association in *T. chinense*. One of the positively associated species, *Eragrostis curvula*, belongs to the Poaceae; thus the present results confirm previous observations that *T. chinense* often occurs in proximity to grasses (Numata and Yoshizawa, 1975). The present study was conducted in natural grassland on a flood-prone riverside of the Kizu

TABLE 1. *List of plant species at the study site with the frequency of occurrence in all plots and in* Thesium *plots*

				Frequency of occurrence (%)	
Species	Growth form[‡]	Native species[§]	Haustorial formation	All plots ($n = 209$)	*Thesium* plots ($n = 60$)
Artemisia capillaris (Asteraceae)[#]	p	n	Yes	125 (59·8)	36 (60·0)
Galium verum (Rubiaceae)[#]	p	n	Yes	59 (28·2)	20 (33·3)
Eragrostis curvula (Poaceae)[#]	p	a	Yes	58 (27·8)	24 (40·0)*
Diodia teres (Rubiaceae)[#]	p	a	Yes	57 (27·3)	9 (15·0)[†]
Lespedeza juncea (Fabaceae)[#]	p	n	Yes	50 (23·9)	23 (38·3)**
Rumex acetosella (Polygonaceae)[#]	p	n	Yes	27 (12·9)	8 (13·3)
Vicia sepium (Fabaceae)[#]	a	n	Yes	26 (12·4)	12 (20·0)
Viola mandshurica (Violaceae)[#]	p	n	Yes	24 (11·5)	5 (8·3)
Briza maxma (Poaceae)	a	a	Yes	14 (6·7)	4 (6·7)
Cerastium glomeratum (Caryophyllaceae)	b	a		11 (5·3)	6 (10·0)
Oxalis corniculata (Oxialidaceae)	p	n	Yes	10 (4·8)	1 (1·7)
Andropogon virginicus (Poaceae)	p	a	Yes	9 (4·3)	1 (1·7)
Erigeron annuus (Asteraceae)	a	n	Yes	8 (3·8)	2 (3·3)
Fabaceae sp. (Fabaceae)	a	a	Yes	7 (3·3)	2 (3·3)
Artemisia princeps (Asteraceae)	p	n	Yes	6 (2·9)	1 (1·7)
Oenothera erythrosepala (Onagraceae)	b	a		6 (2·9)	0 (0·0)
Dianthus superbus (Caryophyllaceae)	p	n	Yes	5 (2·4)	2 (3·3)
Bulbostylis barbata (Cyperaceae)	a	n		5 (2·4)	0 (0·0)
Cymbopogon tortilis (Poaceae)	p	n	Yes	5 (2·4)	2 (3·3)
Leonurus sibiricus (Lamiaceae)	p	n		4 (1·9)	0 (0·0)
Potentilla chinensis (Rosaceae)	p	n	Yes	3 (1·4)	1 (1·7)
Rubia argyi (Rubiaceae)	p	n		3 (1·4)	0 (0·0)
Galium sprium (Rubiaceae)	b	n		3 (1·4)	0 (0·0)
Agrostis sp. (Poaceae)	p	a	Yes	3 (1·4)	1 (1·7)
Sporobolus fertilis (Poaceae)	p	n	Yes	3 (1·4)	1 (1·7)
Pueraria lobata (Fabaceae)	p	n	Yes	3 (1·4)	1 (1·7)
Oenothera laciniata (Onagraceae)	b	a		2 (1·0)	1 (1·7)
Carex sp. (Cyperaceae)	p	n	Yes	2 (1·0)	0 (0·0)
Rumex japonicus (Polygonaceae)	p	n		2 (1·0)	0 (0·0)
Setaria faberi (Poaceae)	a	n		2 (1·0)	0 (0·0)
Lamium purpureum (Lamiaceae)	b	a		2 (1·0)	0 (0·0)
Ambrosia artemisiifolia (Asteraceae)	a	a		2 (1·0)	1 (1·7)
Digitaria adscendens (Poaceae)	a	n		1 (0·5)	0 (0·0)
Erigeron philadelphicus (Asteraceae)	p	n		1 (0·5)	1 (1·7)
Arundinella hirta (Poaceae)	p	n		1 (0·5)	0 (0·0)
Erigeron sumatrensis (Asteraceae)	b	a		1 (0·5)	0 (0·0)
Sedum bulbiferum (Crassulaceae)	b	n	Yes	1 (0·5)	0 (0·0)
Akebia quinata (Lardizabalaceae)	p	n		1 (0·5)	1 (1·7)

[‡] a, Annual; b, biennial; p, perennial.
[§] n, Native; a, alien.
[#] Tested for significance of association using Fisher's exact test.
* $P < 0{\cdot}05$, ** $P < 0{\cdot}01$ positive association with *Thesium* plants.
[†] $P < 0{\cdot}05$ negative association with *Thesium* plants.

River, where many indigenous endangered plant species are found. However, the habitat has recently been invaded by various alien plant species, some of which are also parasitized by *T. chinense*, e.g. *Eragrostis curvula*, *Diodia teres* and *Andropogon virginicus*, further suggesting that there is limited specialization.

Direct observation of the roots revealed a previously unsuspected diversity of host plants for *T. chinense*. Overall, 57·9 % of the plant species that occurred in the population were parasitized by *T. chinense* (Table 1) and they belonged to 11 different families encompassing a broad range of angiosperms, suggesting that specialization to particular host taxonomic groups has not occurred in *T. chinense*. However, an analysis of hosts indicated that species such as *Andropogon virginicus* are strongly preferred and that the Poaceae had considerably more haustoria than expected from their root biomass. One factor that may influence such results is haustorium size because some species may have more but smaller haustoria than other species. The analysis of haustorium size in fact suggested that those that formed on *Lespedeza juncea* and *Pueraria lobata* were larger than those in some other species. However, haustorium size is generally very similar among host species, indicating that the strong preference for *Andropogon virginicus* and Poaceae plants is not associated with haustorium size

The two species that had larger haustoria, i.e. *Lespedeza juncea* and *Pueraria lobata*, both belong to the Fabaceae, the family that had the largest overall haustorium size (Table 5). The reason for the large haustoria sizes is

Table 2. *Observed and expected numbers of* Thesium *haustoria on the roots of various host plants*

	Number of haustoria				
Species	Observed		Expected		χ^2
Lespedeza juncea	956		829·8		19·2
Artemisia capillaris	307		496·2		**72·1**
Dianthus superbus	86		465·3		**309·2**
Potentilla chinensis	14		419·0		**391·5**
Pueraria lobata	193		403·8		**110·0**
Eragrostis curvula	448		395·3		7·0
Cymbopogon tortilis	550		272·5		**282·7**
Carex sp.	42		195·7		**120·7**
Andropogon virginicus	844		188·3		**2283·3**
Rumex acetosella	167		149·3		2·1
Agrostis sp.	318		127·7		**283·8**
Galium verum	25		49·3		12·0
Oxalis corniculata	9		22·9		8·5
Agropyron sp.	1		21·1		19·1
Briza maxima	18		10·5		5·4
Viola mandshurica	30		9·8		**41·8**
Erigeron annuus	60		9·5		**269·4**
Poaceae sp.	5		6·6		0·4
Fabaceae sp.	4	6	3·6	6·7	0·1
Vicia sepium	2		1·6		
Valerianella locusta	0		0·9		
Sedum bulbiferum	0		0·6		
Total	4079		4079		**4238·4**

All species with expected values of <5 are grouped in the calculation of χ^2. Significant chi-squares ($\chi^2 > 28·9$, $P < 0·05$) are in bold.

Table 3. *Observed and expected numbers of* Thesium *haustoria in various host-plant families*

	Number of haustoria		
Family	Observed	Expected	χ^2
Fabaceae	1155	1238·8	5·7
Poaceae	2184	1021·8	**1321·9**
Asteraceae	367	505·7	**38·0**
Caryophyllaceae	86	465·3	**309·2**
Rosaceae	14	419·0	**391·5**
Cyperaceae	42	195·7	**120·7**
Polygonaceae	167	149·3	2·1
Rubiaceae	25	49·3	12·0
Oxialidaceae	9	22·9	8·5
Violaceae	30	9·8	**41·8**
Total	4079	4079	**2251·3**

The expected numbers for Valerianaceae and Crassulaceae were less than five and were thus excluded from the calculation of χ^2. Significant chi-squares ($\chi^2 > 16·92$, $P < 0·05$) are in bold.

unknown, but because these plants fix atmospheric nitrogen they may be of higher nutritional value, allowing haustoria to reach larger sizes. Thus, although these plants were not the preferred hosts as judged by the number of haustoria, they may be suitable hosts for *T. chinense*. However, Jiang *et al.* (2008) showed that in the root hemiparasitic *Rhinanthus minor* nitrogen fixation by the host legume is of no benefit to the parasite. It should therefore be tested explicitly whether *T. chinense* grown on legumes and on non-legumes differ in any significant ways that affect its growth performance, and whether such a difference, if any, is attributable to nitrogen fixation (Gibson and Watkinson, 1991; Marvier, 1996; Matthies, 1996).

Overall, the present results demonstrate that *T. chinense* uses various angiosperm hosts, some of which are more heavily infected than others. Several proximate factors are probably responsible for determining host range and selectivity in *T. chinense*, including the availability of chemical stimulants, strength of host defence, and level of osmotic pressure. Because species of *Thesium* are known to germinate in the absence of host chemical stimulants (Fer *et al.*, 1993, 1994), such a signal is probably not required for seed germination in *T. chinense*. However, chemical stimulants are involved in haustorial formation in root parasites of Orobanchaceae (Musselman, 1980; Westwood, 2000; Yoder, 2001; Bouwmeester *et al.*, 2003). Thus, it is possible that the availability of such signals may determine the success of root infection in *Thesium*. The strength of host defences such as induced lignification may also affect host quality. For example, some parasitic plants such as *Rhinanthus minor* (Cameron *et al.*, 2006; Cameron and Seel, 2007; Rumer *et al.*, 2007) and *Orobanche crenata* (Perez-de-Luque *et al.*, 2005) are more likely to establish successful haustorial formation with less-defended plants. In addition, parasitic plants usually have higher root osmotic pressure than do their hosts, thereby facilitating water movement from host to parasite (Harris and Lawrence, 1916; Gworgwor and Weber, 1991; Simier *et al.*, 1993; Williamson *et al.*, 2002). Thus, it is possible that host plants vary greatly in these physiological attributes, which may be important for determining the pattern of host use in *T. chinense*.

Overall, the finding that *T. chinense* parasitizes an array of angiosperm hosts has broad general implication for patterns of host use in root parasites of Santalales. Although the present data suggest that *T. chinense* has strong host selectivity, it has obviously not become specialized to a limited number of preferred hosts. This is in marked contrast with some holoparasites such as *Rafflesia*, which has an extremely narrow host range (Ismail, 1988). Other members of Santalales are also known to use a broad range of angiosperms; for example, *Osyris alba* uses 23 host species belonging to 14 families (Jamal, 2006). Nevertheless, the host ranges of many Santalales species are still little understood, and many reported cases of host associations are probably fragmentary. For example, the holoparasitic *Balanophora tobiracola* (Balanophoraceae) is known to parasitize species of *Pittosporum* (Pittosporaceae), *Ligustrum* (Oleaceae), *Eurya* (Theaceae), *Celastrus* (Celastraceae) and *Rhaphiolepis* (Rosaceae; Akuzawa, 1982; Kawakita and Kato, 2002), but considering that these hosts belong to divergent families and are often dominant trees in the vegetation, it is possible that other plants are also used by *B. tobiracola*. Thus, the host ranges of Santalales species (especially the hemiparasitic species) are probably much broader than currently known, as evidenced by the present results for *T. chinense*, which was thought to parasitize only grasses. The evolutionary significance of a wide host range is yet unknown, but may be related to the generally large seed size in Santalales

TABLE 4. *Size distributions of* Thesium *haustoria found on the roots of each host species*

Species no.	Species	Size range (mm)						Significance
		<1·0	1·0–1·5	1·5–2·0	2·0–2·5	2·5–3·0	>3·0	
1	*Lespedeza juncea*	548	259	106	40	3	0	2, 3, 4, 5, 8, 9
2	*Andropogon virginicus*	659	136	41	7	1	0	1
3	*Cymbopogon tortilis*	410	111	18	8	2	1	1
4	*Eragrostis curvula*	368	75	4	1	0	0	1
5	*Agrostis* sp.	259	54	5	0	0	0	1
6	*Artemisia capillaris*	214	69	23	1	0	0	
7	*Pueraria lobata*	124	37	17	12	3	0	8
8	*Rumex acetosella*	149	16	2	0	0	0	1,7
9	*Dianthus superbus*	74	11	1	0	0	0	1
10	*Erigeron annuus*	48	12	0	0	0	0	
11	*Praecoces* sp.	38	4	0	0	0	0	
12	*Viola mandshurica*	28	2	0	0	0	0	
13	*Galium verum*	24	1	0	0	0	0	
14	*Briza maxima*	18	0	0	0	0	0	
15	*Potentilla chinensis*	12	2	0	0	0	0	
16	*Oxalis corniculata*	9	0	0	0	0	0	
17	Poaceae sp.	5	0	0	0	0	0	
18	Fabaceae sp.	4	0	0	0	0	0	
19	*Vicia sepium*	1	1	0	0	0	0	
20	*Agropyron* sp.	1	0	0	0	0	0	

The size distributions were significantly different among species (Kruskal–Wallis test, $P < 0{\cdot}0001$). Pairs of species that had significant differences in the sizes of *Thesium* haustoria (Scheffe's test, $P < 0{\cdot}05$) are indicated by species number.

TABLE 5. *Size distributions of* Thesium *haustoria for each host-plant family*

Family no.	Family	Size range (mm)						Significance
		<1·0	1·0–1·5	1·5–2·0	2·0–2·5	2·5–3·0	>3·0	
1	Fabaceae	1720	376	68	16	3	1	2
2	Poaceae	677	297	123	52	6	0	1, 3, 4, 5, 6, 7, 8
3	Asteraceae	262	81	23	1	0	0	2,4
4	Polygonaceae	149	16	2	0	0	0	2,3
5	Caryophyllaceae	74	11	1	0	0	0	2
6	Cyperaceae	38	4	0	0	0	0	2
7	Violaceae	28	2	0	0	0	0	2
8	Rubiaceae	24	1	0	0	0	0	2
9	Rosaceae	12	2	0	0	0	0	
10	Oxalidaceae	9	0	0	0	0	0	

The size distributions were significantly different among families (Kruskal–Wallis test, $P < 0{\cdot}0001$). Pairs of families that had significant differences in the sizes of *Thesium* haustoria (Scheffe's test, $P < 0{\cdot}05$) are indicated by family number.

(Moles *et al.*, 2005), which limits the number of seeds produced per plant and hence the chance of arriving at preferred hosts. Further studies of the life history and host associations in other members of the Santalales should broaden the perspectives on patterns of parasitic evolution in this intriguing plant lineage. Moreover, pot-based comparisons of performance on different hosts, or histological investigations of haustorial anatomy would provide further insights into the ecology of parasitic life style in plants of the Santalales.

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