The host range and selectivity of a parasitic plant: *Rhinanthus minor* L.

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Summary. *Rhinanthus minor* (Yellow-rattle) is a widespread hemiparasitic plant of grassland habitats throughout Britain. Association analysis of the dune vegetation at Holme-next-the-Sea in eastern England revealed only two potential host plants through positive association. In contrast direct examination of the root systems revealed haustorial connections with 20 host species. The number of species parasitized by one plant ranged from one to seven. Data from another four sites in Britain and one in central Europe indicate that the natural host range of *R. minor* encompasses at least 50 species from 18 families with 22% in the Leguminosae and 30% in the Gramineae. Comparison of the number of haustorial connections made to each species with the abundance of roots in the soil shows that *R. minor* is a highly selective parasite, but that the selectivity is not consistent between populations or between plants from different parts of the same population. The reasons for host selectivity are discussed.

Key words: *Rhinanthus* – Hemiparasitism – Host selectivity

It is easy to establish the host range of an aerial parasitic plant: one simply has to identify the species on which it is growing. It is, however, rather more difficult to identify the hosts of parasites attached to below-ground structures. Two basic methods have been employed to this end. One is an indirect method which involves collecting data on the communities that contain parasites, to see if any species are more frequently associated with the parasite than would be expected by chance (Chuang and Heckard 1971; Hodgson 1973). A second (Piehl 1963; Musselman and Mann 1977) is to examine the roots directly and to locate those species to which the parasites are attached.

The number of hosts recorded by the root examination technique for hemiparasitic members of the Scrophulariaceae ranges from four to seventy-nine (Table 1). In addition, other hosts have been inferred from association studies, and other species, including some from outside the geographical range of the parasites, have acted as hosts

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in cultivation experiments. Clearly many of the parasitic Scrophulariaceae are capable of using a wide range of hosts. There is, however, far less information on the degree of selectivity shown by the parasites between hosts (Sprague 1962; Piehl 1963; Smith 1963). Following a study of 27 taxa of hemiparasitic Scrophulariaceae, Weber (1967a) suggested that certain families were preferred as hosts (Rosaceae, Leguminosae, Labiatae, Compositae, Cyperaceae and Gramineae), while others (e.g. Orchidaceae) were completely avoided. Similarly, Chuang and Heckard (1971) found that *Cordylanthus* species parasitized up to four principal genera of species, again signifying some preference on the part of the parasite. But in no case has the problem been addressed statistically by means of a comparison between

Table 1. The number of species recorded as hosts in the field for a range of hemiparasitic Scrophulariaceae. Self-parasitism (a) and attachment to non-living material (b) are also indicated

Species	Number of host species recorded	Reference
Aureolaria pedicularia	15	Musselman and Mann (1977)
Castilleja coccinea	18 b	Malcolm (1966) Musselman and Mann (1977)
Dasistoma macrophylla	4 a	Piel (1962a) Musselman and Mann (1977)
Euphrasia salisburgensis	8	Crosby-Browne (1950)
Melampyrum arvense	12	Weber (1976a)
Melampyrum lineare	17 a, b	Piehl (1962b) Cantlon et al. (1963) Musselman and Mann (1977)
Pedicularis canadensis	79 a, b	Piehl (1963)
Pedicularis palustris	6	Weber (1976a)
Rhinanthus alectorolophus	17	Weber (1976a)
Rhinanthus aristatus	8	Weber (1976a)
Rhinanthus halophilus	7	Weber (1976a)
Rhinanthus minor	26	Weber (1976a)

the frequency of attachment to each species and the availability of each potential host species.

The aims of this paper are 1) to quantify the host range of the root hemiparasite, *Rhinanthus minor* (Scrophulariaceae), by means of both association analysis and direct examination of the roots and 2) to quantify host selectivity by comparing the number of haustorial connections made to each species by *R. minor* with the abundance of each species' roots in the soil.

Methods

The parasitic behavior of *Rhinanthus minor* was investigated in three areas of the dune system at Holme-next-the-Sea, Norfolk (National Grid References TF 696440, TF 695441, TF 694439). In each part of the colony, the host range was examined by both direct and indirect methods.

Association analysis

The indirect method consisted of a quadrat-based association analysis. In each area, two hundred 10×10 cm quadrat samples were taken. One hundred quadrats were placed over randomly selected *R. minor* plants at the time of flowering in June 1982. For each of these quadrats, a paired sample was taken after the quadrat had been moved to a randomly determined position, which contained no *R. minor*, within 1 m of the original quadrat. The presence of every species in each quadrat was recorded, and the data were analysed for any significant species associations by means of contingency χ^2. Only those species which occurred in more than ten quadrats at a site were tested for association with *R. minor*.

Examination of roots

The direct method by which the parasitic behaviour of *R. minor* was examined was similar to that used by Weber (1976a) and Musselman and Mann (1977), in that the haustorial connections were located by tracing the roots of the parasite. The host species was then determined by tracing the host root back to the shoot, although with practice it became possible to identify most hosts by the colour and form of their roots. As studies *in situ* lead to a high frequency of root breakage, turves containing *R. minor* were first removed to the laboratory where the soil was loosened by soaking for 24 hours. It was then possible with careful dissection and washing to locate intact parasite-host connections. A total of 14 turves were examined in this way, five from each of two areas and four from the third. A preliminary investigation indicated that most host plants were found within 10 cm of the parasite. Turves containing between two and eight *R. minor* plants, with 10 cm around each specimen of *R.minor* were, therefore, used. The turves were excavated to a depth of 10 cm. A total of 19, 25 and 21 *R. minor* plants were examined from the three areas.

After as many haustoria as possible had been located, all of the soil was washed from the turf, and the roots of all the constituent species were separated out. The roots were dried in an oven at 70° C for three days and then weighed to determine the relative frequency by weight of the roots of each species in the turf.

In order to demonstrate any host selectivity on the part of the parasite, it needs to be shown that *R. minor* attacks a species more or less frequently than would be expected by chance. A suitable Null Hypothesis to test is that *R. minor* is a generalist parasite in that it attacks each species with a frequency in direct proportion to the frequency of the species' roots in the turf. The observed and expected number of haustoria can then be compared by means of a χ^2 test. It is assumed here that all roots are available to the parasite as haustorial connections were formed with both very fine rootlets and large tap roots.

In addition to the detailed survey of host range and selectivity at Holme-next-the-Sea, a general survey of host species was conducted by examining turves from a range of sites and habitats throughout Britain: sand dunes at Aberffraw, Anglesey (Nat. Grid Ref. SH 364684); calcareous grassland near Bridlington, North Humberside (Nat. Grid Ref. TA 164669); neutral grassland at Strensall, North Yorkshire (Nat. Grid Ref. SE 658626); and coastal pasture at Fernaig, Wester Ross (Nat. Grid Ref. NG 845345).

Results

Association analysis

Only two species at one site were found to be significantly positively associated with *Rhinanthus minor*: *Ononis repens* and *Plantago lanceolata* at site H3 (Table 2). In contrast 11 species showed a negative association.

Examination of roots

The dissection of the turves demonstrated that a wide range of species were parasitized by *Rhinanthus minor* on the dunes at Holme-next-the-Sea (Table 3a) and on the four other sites around Britain (Table 3b). In total, haustorial connections were recorded with 34 species of host. In addition, haustoria that were non-functional, at least in the parasitic sense, were observed attached to an old testa of *R. minor*, the dead rhizomes of *Carex arenaria* and to rhizoids of *Dicranum scoparium*. Self-parasitism, both within one

Table 2. The species which a χ^2 test showed to be significantly associated with *Rhinanthus minor* in three areas of the sand dunes at Holme-next-the-Sea

Site	Positively associated	Negatively associated
H1	–	*Rumex acetosella**
		*Hypnum cupressiforme**
H2	–	*Vicia sativa***
		*Tortula ruraliformis***
		*Honkenya peploides***
		*Cerastium semidecandrum**
H3	*Ononis repens****	*Elymus farctus****
	*Plantago lanceolata****	*Hypnum cupressiforme****
		*Sedum acre***
		*Bromus hordeaceus***
		*Carex arenaria**
		*Trifolium arvense**

$* P < 0.05; ** P < 0.01; *** P < 0.001$

Table 3a–c. A list of the species recorded as hosts for *Rhinanthus minor* by examination of the roots in **a** fourteen turves from the sand dunes at Holme-next-the-Sea, together with additional species recorded from **b** a range of sites and habitats throughout Britain (see text for details) and **c** by Weber (1976a)

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a	*Achillea millefolium*	*Hieracium pilosella*
	Anthoxanthum odoratum	*Honkenya peploides*
	Arenaria serpyllifolia	*Koeleria macrantha*
	Bromus hordeaceus	*Lotus corniculatus*
	Carax arenaria	*Ononis repens*
	Cerastium semidecandrum	*Plantago lanceolata*
	Daucus carota	*Poa pratensis*
	Elymus farctus	*Sedum acre*
	Festuca rubra	*Trifolium campestre*
	Galium verum	*Vicia lathyroides*
b	*Agrostis capillaris*	*Lolium perenne*
	Agrostis stolonifera	*Medicago lupulina*
	Dactylis glomerata	*Potentilla reptans*
	Deschampsia cespitosa	*Ranunculus repens*
	Fraxinus exelsior	*Rubus fruticosus* agg.
	Holcus lanatus	*Salix repens*
	Hypochaeris radicata	*Trifolium repens*
c	*Brachypodium pinnatum*	*Luzula campestris*
	Coronilla varia	*Melampyrum cristatum*
	Cynosurus cristatus	*Poa trivialis*
	Cytisus scoparius	*Populus nigra*
	Echium vulgare	*Prunella grandiflora*
	Knautia dipsacifolia	*Trifolium dubium*
	Koeleria pyramidata	*Trifolium montanum*
	Leontodon hispidus	*Trifolium pratense*
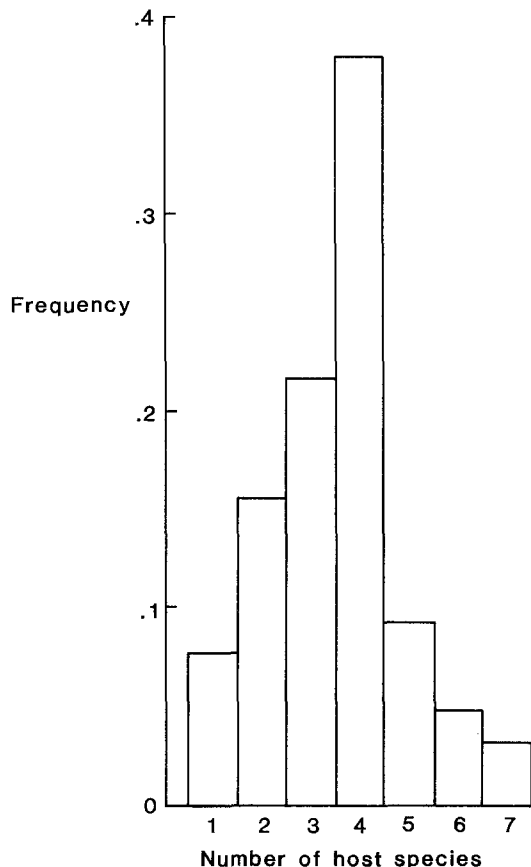
Fig. 1. Frequency distribution of the number of host species of 65 plants of *Rhinanthus minor* from three sites on the sand dunes at Holme-next-the-Sea

plant and between neighbouring plants, was recorded infrequently. Of the 65 plants examined at Holme-next-the-Sea, only five were attached to just one host whilst two plants were attached to at least seven different host species. The most frequent number of host species was four per plant (Fig. 1).

The data which relate to the frequency of attachment of *R. minor* to each species in the turf, with the corresponding expected values, are presented in Table 4 as the summed data for each site. *R. minor* is clearly not a non-selective parasite: in every case the value of χ^2 is highly significant ($P < 0.001$). Some of the species contribute a larger proportion to the total χ^2 value than others, and those which contribute more than a subjectively chosen value of five to the total χ^2 value for a site are classified as either 'preferred' or 'avoided', according to whether they have more or fewer connections than expected. Table 5 contains a list of the preferred and avoided species at each site. It should be noted that *Poa pratensis* and *Ononis repens* appear as preferred hosts at one site and avoided hosts at another. This may simply reflect the fact that *Poa pratensis* and *Ononis repens* were much commoner at the sites of putative 'avoidance' and, therefore, less likely to be parasitized overall, as a proportion. Also the species classified as avoided hosts were not strictly avoided: only *Trifolium micranthum* and *Luzula campestris* have not been recorded as hosts at Holme-next-the-Sea.

Discussion

Indirect methods which involve an examination of the above-ground spatial relationships of potential host species and the parasite have frequently been used in an attempt to define the host range of a parasite (e.g. Chuang and Heckard 1971). On the basis of the positive associations detected in this study (Table 2) it might be concluded that the only hosts of *R. minor* on the dunes at Holme-next-the-Sea were *Ononis repens* and *Plantago lanceolata*. Yet the dissection of the roots indicated that 18 species in addition to *O. repens* and *P. lanceolata* were parasitized by *R. minor*. Six of the negatively associated species were also found to be parasitized. Association analysis is clearly an inappropriate means of detecting the host preferences of *R. minor*.

There are several possible reasons why so few positive associations were observed. Perhaps the most likely explanation, at least of abundant hosts, is that the parasite is not numerous enough to attack a significantly large proportion of the host population for the association to be statistically significant. The much larger number of significant negative associations (Table 2) could be explained in several ways. Firstly, the parasitic interaction may be sufficiently deleterious to kill or severely suppress the host (Atsatt and Strong 1970) – in this case a negative association rather than a positive one is indicative of parasitism. Secondly, the species which are negatively associated with *R. minor* may have optimal conditions that are outside the environmental tolerance limits of *R. minor*. *Elymus farctus*, for example, thrives in conditions of limited sand accretion (Ranwell 1972), and most of the annual plants and mosses listed in Table 2 are restricted to the less competitive open patches on a dune. *R. minor*, in contrast, is intolerant of sand accretion (Gibson, unpublished data) and is dependent for its survival on the high root density provided by perennial vegetation. Problems in defining the causes of associa-

Table 4. The observed and expected number of haustorial connections between *Rhinanthus minor* and each species in turves from three sites on the sand dunes at Holme-next-the-Sea. In the calculation of χ^2 all species with expected values of less than five are grouped

	Number of haustoria		χ^2
	Observed	Expected	
Site H1			
Galium verum	138	163.1	3.9
Koeleria macrantha	231	140.6	58.1
Poa pratensis	39	110.0	45.8
Plantago lanceolata	75	48.7	14.2
Festuca rubra	21	33.5	4.7
Elymus farctus	15	30.7	8.0
Anthoxanthum odoratum	40	20.1	19.7
Hieracium pilosella	13	18.1	1.4
Daucus carota	7	13.1	2.8
Trifolium micranthum	0	8.5	8.5
Sedum acre	12	8.1	1.9
Luzula campestris	0	7.1	7.1
Rumex acetosella	0 ⎫	4.1 ⎫	
Lotus corniculatus	3 ⎪	2.5 ⎪	
Bromus hordeaceus	4 ⎪	1.2 ⎪	
Aira praecox	0 ⎬ 19	0.6 ⎬ 9.3	10.1
Vicia lathyroides	6 ⎪	0.4 ⎪	
Trifolium campestre	6 ⎪	0.4 ⎪	
Hypochaeris radicata	0 ⎭	0.1 ⎭	
		186.2 ($P < 0.001$; 12 d.f.)	
Site H2			
Elymus farctus	267	254.7	0.6
Poa pratensis	305	207.3	46.0
Festuca rubra	146	205.9	17.4
Carex arenaria	57	152.1	59.5
Ononis repens	13	43.4	21.2
Plantago lanceolata	45	35.8	2.4
Honkenya peploides	68	25.0	74.0
Galium verum	9 ⎫	3.1 ⎫	
Crepis capillaris	0 ⎪	1.8 ⎪	
Cerastium semidecandrum	3 ⎪	1.4 ⎪	
Arenaria serpyllifolia	1 ⎪	1.0 ⎪	
Sedum acre	0 ⎬ 32	0.6 ⎬ 8.8	61.2
Myosotis ramosissima	0 ⎪	0.3 ⎪	
Valerianella locusta	0 ⎪	0.3 ⎪	
Hypochaeris radicata	0 ⎪	0.2 ⎪	
Vicia lathyroides	19 ⎪	0.1 ⎪	
Phleum arenarium	0 ⎭	0.0 ⎭	
		282.3 ($P < 0.001$; 7 d.f.)	

Table 4 (continued)

	Number of haustoria		χ^2
	Observed	Expected	
Site H3			
Elymus farctus	56	195.4	99.4
Ononis repens	281	131.4	170.3
Festuca rubra	38	114.2	50.8
Galium verum	164	103.8	34.9
Plantago lanceolata	42	45.1	0.2
Poa pratensis	38	35.7	0.1
Achillea millefolium	13	13.4	0.0
Carex arenaria	15	12.1	0.7
Potentilla reptans	0 ⎫	2.4 ⎫	
Arenaria serpyllifolia	0 ⎬ 7	0.8 ⎬ 3.8	2.7
Cerastium semidecandrum	7 ⎪	0.6 ⎪	
Phleum arenarium	0 ⎭	0.0 ⎭	
		359.1 ($P < 0.001$; 8 d.f.)	

Table 5. The preferred and avoided hosts of *Rhinanthus minor* at three sites on the sand dunes at Holme-next-the-Sea

Site	Preferred hosts	Avoided hosts
H1	*Koeleria macrantha* *Plantago lanceolata* *Anthoxanthum odoratum*	*Poa pratensis* *Elymus farctus* *Trifolium micranthum* *Luzula campestris*
H2	*Poa pratensis* *Honkenya peploides*	*Festuca rubra* *Carex arenaria* *Ononis repens*
H3	*Ononis repens* *Galium verum* .	*Elymus farctus* *Festuca rubra*

tions are further confounded by associations with other species. For example, if a species A is negatively associated with *R. minor*, but positively associated with species B, which is independent of *R. minor*, then species B will display a spurious negative association with *R. minor*.

It is clear that any attempt to define the host range of parasitic plants must involve direct examination of the root system, except perhaps if the parasite is highly selective. In this study 34 species of host were identified (Tab-

le 3a, b) to which can be added the 16 additional species recorded by Weber (1976a) for *R. minor*, including *R. minor* var. *balticus*, in Central Europe (Table 3c), a total of 50 species. These include a range of species with different life-histories and growth forms: there are nine species of annual or short-lived perennial, 36 species of herbaceous perennial and five woody species. Eighteen families are represented in the list of hosts, each by up to four species, with the exception of Leguminosae (11 species) and the Gramineae (16 species). These two families are among those considered to be the preferred hosts of 27 taxa of European hemiparasitic Scrophulariaceae by Weber (1976 a). Likewise, Hodgson (1973) considered that more than half of the hosts of *Rhinanthus minor*, *Euphrasia officinalis* agg. and *Odontites verna* belong to Leguminosae and Gramineae.

Although most hosts are members of the Gramineae and Leguminosae, this may be for different reasons in the two families. Grasses are generally the most common components of the communities in which *R. minor* is found. High fitness may, therefore, result from attachment to these species, as the probability of locating a suitable host is always very high. In contrast, legumes are normally much less frequent than grasses in these communities, but they

are capable of fixing atmospheric nitrogen, and as a consequence are relatively independent of soil nitrogen conditions. A parasite which is capable of abstracting nitrogeneous compounds from a leguminous host will, therefore, be more fit than one which is attached only to species that are entirely dependent on soil nitrogen. Certainly species such as *Rhinanthus* may display a high degree of tolerance to low nitrogen conditions (Fresco 1980) perhaps because of their parasitism of legumes.

The haustorial connections to most of the host species in this study were very similar in both size (ca. 1 mm in diameter) and structure. Weber and Weberling (1975) similarly concluded, following a study of 30 taxa of hemiparasitic Scrophulariaceae, that the haustoria of each species are morphologically similar amongst plants of the same age, even if the habitats or hosts are different. Those to *Festuca rubra* were, however, frequently very much smaller, resembling the structures termed wart-haustoria by Weber and Weberling (1975). In contrast, haustorial connections to *Lotus corniculatus*, were generally larger than normal with a diameter of 2 mm or more, so that they resembled root nodules. Although it is possible that some of the morphological differences between haustoria were due to differences in the age of the parasites, one plant which was attached to both *Festuca* and *Lotus* demonstrated both types of haustorial connection. No structures comparable with metahaustoria (Weber 1976b) were observed.

When the number of haustorial connections to the roots of each species are compared with the abundance of roots in the soil (Table 4), it is quite clear that *R. minor* demonstrates considerable selectivity among its potential hosts. Preferred hosts included species from the Caryophyllaceae, Gramineae, Leguminosae, Plantaginaceae and Rubiaceae whilst avoided hosts were from the Cyperaceae, Gramineae, Juncaceae and Leguminosae (Table 5). Thus whilst members of the Gramineae and Leguminosae are commonly parasitized, *R. minor* nevertheless shows considerable selectivity between members of these two families. Also it is clear that the preference or avoidance of particular species by the hemiparasite cannot be seen as absolute, but rather as relative to the other species in the community. Both *Ononis repens* and *Poa pratensis* were preferred hosts at one site and avoided at another. Amongst the avoided hosts only *Luzula campestris* and *Trifolium micranthum* were not parasitized at all.

One of a potential number of sources of error in the determination of host selectivity might arise from the morphological variability of haustoria. It might be assumed, as some haustorial connections are inevitably broken during the dissection of the turves, that there would be selective breakage of the smaller haustoria, and that those species with smaller haustoria (e.g. *Festuca rubra*) would appear to be avoided. This possibility cannot be refuted, but it is a problem common to all studies of this nature. The weight of roots may also not be the best measure of root abundance. It would, therefore, be particularly interesting to compare the number of haustorial connections with the length of root for each species.

The most likely reason why *R. minor* shows host selectivity is that the parasite has special nutritional requirements that can be supplied only by particular hosts, as was suggested previously for the high frequency of leguminous hosts. This would appear to be the reason why *Pedicularis densiflora* and *P. semibarbata* parasitize only woody hosts (Sprague 1962). These two species occupy a very arid habitat, so that woody species with deep rooting systems are the only hosts that can supply sufficient water and nutrients to the parasites. A similar situation was noted in this study on a Welsh sand dune system where one of the preferred hosts of *R. minor* was *Salix repens*, presumably one of the few species with a sufficiently extensive root sysem to supply water throughout the summer drought. The mechanism by which such positive selectivity occurs in this case remains unknown. It is possible that the growth of the parasite root might be stimulated by substances exuded from the roots of the host (Kuijt 1969), but the only study to date which suggests that exudates may affect *Rhinanthus* is in relation to the delayed germination of seeds stratified amongst the roots of certain hosts (de Hullu 1985). Most of the other means that have been put forward to explain selectivity relate to mechanisms, such as biochemical and physical barriers (Kuijt 1969), which prevent the utilization of certain hosts.

Rhinanthus minor is clearly not specific in its host attachments as parasitic connections have been observed with a wide range of host species. It has, however, been demonstrated that the parasite exercises some selectivity in the hosts that it utilizes, so that some species are more frequently attacked than one might expect by chance, although the selectivity is not consistent between populations or between plants from different parts of the same population. This selectivity may have important consequences for the communities in which *R. minor* grows (Watkinson and Gibson 1988), as it provides a mechanism by which the parasite can selectively depress the performance of components of the community and so have an important effect on community structure.

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