

## The role of the hemiparasitic annual *Rhinanthus minor* in determining grassland community structure

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Received April 10, 1991 / Accepted in revised form August 2, 1991

**Summary.** *Rhinanthus minor* (yellow-rattle) is a widespread hemiparasitic plant of grassland habitats throughout Great Britain. It is usually considered to be indicative of species-rich grassland, but in a survey of 14 habitats throughout Britain it was found that *R. minor* at the time of flowering normally occupied relatively low-diversity patches within areas of high diversity as determined by the number of species, Simpson's Index and the Shannon-Wiener Index. Following the death of adult plants of *R. minor* in the summer it was shown that the pattern of species diversity changed such that by the time *R. minor* germinated in the following spring the differences between the areas containing and not containing *R. minor* were much less distinct. A perturbation experiment in which *R. minor* was removed from four sites indicated that the effect of the removal of *R. minor* on the development of community structure over the next year was to increase species diversity on three of the sites and decrease it on the fourth. Those species which responded to the removal of *R. minor* by an increase in abundance were shown to be preferred hosts. All three lines of evidence point to the fact *R. minor* has a significant effect on the species diversity of the communities in which it grows by selectively parasitizing components of the flora and modifying the competitive relationships between plants. However, as the communities generally responded to the removal of *R. minor* by an increase in diversity and as the general survey indicated that *R. minor* is generally associated with areas of low diversity it would appear that the plants which are selectively parasitized are generally not the competitive dominants in the community.

**Key words:** *Rhinanthus* – Hemiparasitism – Species diversity – Community structure

Whilst it is widely recognized that predation, herbivory and competition for resources may play major roles in shaping the structure of plant and animal communities rather less is known of the role of parasitism. Most studies on parasites to date have concentrated on aspects of the dynamic interaction between host and parasite (Hassell and Anderson 1989) without considering wider effects on the community. Where zoologists have considered the effects of host-parasite interactions on community structure, this has generally been in the laboratory, in which community structure is highly simplified. For example, Park (1948), working with flour beetles, *Tribolium* spp., showed that when mixed populations of *T. confusum* and *T. castaneum* were established, *T. castaneum* tended to dominate and ultimately exclude *T. confusum* although the outcome was dependent, to some extent, on the starting densities of the two host species. However, if a parasite *Adelina tribolii* was introduced into the cultures, the population levels of *T. castaneum* were severely depressed, with the result that the two *Tribolium* species were able to coexist, although again the outcome was dependent on the initial densities.

Two studies of plants under glasshouse conditions have similarly demonstrated the effect of a parasitic pathogen on simplified communities. Burdon et al. (1984) exposed mixtures of two genotypes of *Chondrilla juncea* to the rust fungus *Puccinia chondrillina*. One genotype was resistant and the other susceptible to attack by the pathogen. In uninfected mixtures, the susceptible genotype proved to be competitively dominant, but infection by the rust shifted the competitive balance in favour of the resistant genotype. Likewise, Burdon and Chilvers (1977) investigated the effects of the powdery mildew that infects barley, *Erysiphe graminis*, on the interaction between wheat and barley. In uninfected mixtures, barley was dominant and eventually excluded wheat, but in infected mixtures, the performance of barley was sufficiently depressed to permit the coexistence of the two species. Similarly under field conditions diseased individuals are weakened in competition with

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healthy individuals of *Senecio vulgaris* (Paul and Ayres 1986).

It can be concluded from these studies that a parasite or pathogen can influence the competitive interaction between a pair of genotypes or species and in particular that infection of a superior competitor by a parasite can enable an otherwise excluded inferior competitor to coexist (Anderson and May 1986): coexistence is not, however, an inevitable outcome (Gates et al. 1986). This implies that there is at least the potential for such organisms to play a structuring role in the community, and have an effect on, for example, species diversity. Indeed there are many anecdotal accounts of the impact of parasite invasions on the abundances of species (Anderson and May 1986). In few instances, however, do such accounts provide quantitative information on species abundance and diversity. These few include the impact of the soil-borne root pathogen *Phytophthora cinnamomi* on a range of communities in Australia (Newhook and Podger 1972; Weste 1981) and the near extermination of the American chestnut tree *Castanea dentata* by the fungal pathogen *Endothia parasitica* (Day and Monk 1974; Roame et al. 1986).

The role of parasitic plants in determining the structure of natural communities has rarely been considered. In a study of the root hemiparasite *Rhinanthus minor* Gibson and Watkinson (1989) have shown that whilst the plant may parasitize a wide range of hosts it nevertheless shows considerable selectivity. Such selectivity may have important consequences for the communities in which *Rhinanthus* grows, as it provides a mechanism by which the parasite can selectively depress the performance of components of the community, thus affecting the competitive relationships between plants. Indeed Gibson and Watkinson (1991) demonstrated that the competitive relationship between pairs of species was considerably affected by the hemiparasite in various binary mixtures of potential host grown with or without *R. minor*. Nevertheless it remains to be established what role the hemiparasite plays in determining the structure and diversity of plant communities in which it grows. Agriculturalists have noted for a long time that vegetation is low and open in places dominated by the root hemiparasite *Rhinanthus*, although ter Borg (1985) has questioned whether the vegetation is open because of the presence of the hemiparasite, or whether the hemiparasite is present because the vegetation is rather low and open. A more direct test of the effects of hemiparasites on plant community structure comes from experiments in which the density of the hemiparasite has been manipulated. Two experiments which have involved the removal of the hemiparasite *R. angustifolius* from vegetation have shown that the effect is to increase total yield and also to alter the proportion of the component species (Rabotnov 1959; ter Borg and Bastiaans 1973). The most significant change in the vegetation was to increase the proportion of Leguminosae. The effects on the other components of the vegetation varied but unfortunately only very broad categories of species were recognized, such as "other dicots". These data, whilst pointing towards an effect of

the hemiparasite on species diversity, do not allow quantification of the effects.

The aim of this study is to examine the influence of the root hemiparasite *Rhinanthus minor* on the community structure of a range of grasslands and to relate those effects to the selectivity of the parasite and the competitive relationships of the plants. Two approaches have been used. The first involved observations on the species diversity in a range of natural communities in areas with and without *R. minor* whilst the second involved the removal of *R. minor* from areas of vegetation and the monitoring of subsequent changes in species diversity.

## Methods

### *Observations of natural communities*

The species diversity in areas with and without *Rhinanthus minor* was investigated at 14 sites throughout Britain, encompassing a range of habitats. Data were collected on sand dunes at Aberffraw, Anglesey (A: National Grid reference SH 364684), coastal pasture at Fernaig, Wester Ross (F: NG 845345), calcareous grassland at Bessingby (B1, B2: TA 164669) and Flamborough Head (FH1–FH4: TA 256706), North Humberside and neutral grassland at Strensall, North Yorkshire (S1–S6: SE 658626). At each site, data were gathered during June and July 1980 from an area of approximately 0.5 ha.

Communities with and without *R. minor* were characterised by means of a paired quadrat technique. The quadrat was placed over a randomly selected plant of *R. minor*, so that the target plant was located centrally. Preliminary investigations of the roots had indicated that virtually all host plants were located within 10 cm of the parasite. Consequently a 20 × 20 cm quadrat was used in this study. All species present in the quadrat were recorded. The quadrat was then moved to a random position within 1 m of the target plant. If the quadrat in its new position contained no *R. minor* plants, the presence of all species in the quadrat was recorded as previously. If the quadrat in its new position contained any *R. minor* plants, it was relocated as before until it fell in a position where no *R. minor* plants were included. This paired sampling procedure was repeated up to 125 times at each site.

The same procedure involving 100 paired samples was also carried out at four further sites in late June 1982 and again in late April 1983. Three of the sites were on the sand dunes at Holme-next-the-Sea, Norfolk (H1: TF 696440, H2: TF 695441, H3: TF 694439) whilst the other was a base-rich grazing marsh at Strumpshaw Fen, Norfolk (SF: TG 339063).

### *Perturbation experiment*

A perturbation experiment was established at Holme and Strumpshaw in order to investigate the effects on the community of the removal of *R. minor*. In July 1983, before seed was released, all of the *R. minor* plants were cleared from an area of 4 × 4 m at each of the four sites. The areas were chosen on the basis that the vegetation appeared to be more or less homogeneous. In June 1984, the community within each area was then compared with that immediately outside the cleared area. Only the central 2 × 2 m of each area was sampled as there had been some dispersal of seed from outside the cleared area, mostly into a 50-cm strip around the edge. A point quadrat sampling technique was used to ascertain the abundance of all species in the communities. Each point quadrat consisted of a needle which was lowered vertically into the sward 100 times in randomly determined positions within an area of 0.5 m<sup>2</sup>. Each contact between the needle and a piece of live vegetation was recorded. At each dune site, ten quadrat samples of 100 points were recorded, five replicates within the cleared area and

five outside, but within 1 m of the cleared area. At Strumpshaw, only one set of 100 points was recorded from inside the cleared area, and one set from outside the cleared area, because of the much greater sward density at that site.

## Results

### Observations of natural communities

Three species diversity indices were calculated for the community data:  $M$ , the mean number of species per quadrat; Simpson's Diversity Index  $C$ ; and the Shannon-Wiener Index  $H'$ . These indices were calculated for the communities of higher plants (as determined in June or July) in the presence and absence of *R. minor* at each of the 18 sites (Tables 1 and 2a). In almost every case, diversity was lower in communities which contained *R. minor* than in immediately adjacent communities without *R. minor*, i.e. the values of  $M$  and  $H'$  were higher and  $C$  was lower. Only at two sites was there any indication that diversity might be higher in areas of *R. minor*: at site FH1 the species richness was slightly higher in the presence of the hemiparasite whilst at site S4 the Shannon-Wiener index was very slightly higher.

At the four sites in Norfolk for which more detailed

**Table 1.** Diversity indices calculated for communities with (+) and without (–) *Rhinanthus minor* at 14 sites throughout Britain at: Aberffraw, Anglesey (A), Bessingby, North Humberside (B1, B2), Fernaig, Wester Ross (F), Flamborough Head, North Humberside (FH1 to FH4) and Strensall, Yorkshire (S1–S6).  $M$ , mean number of species per quadrat;  $C$ , Simpson's Index;  $H'$ , Shannon-Wiener Index. Those pairs of indices for which diversity is higher in the presence of *R. minor* are marked\*

Site	<i>Rhinanthus</i>	$M$	$C$	$H'$
A	+	8.43	0.060	3.11
	–	10.86	0.041	3.40
B1	+	6.87	0.082	2.71
	–	8.00	0.071	2.81
B2	+	5.57	0.068	2.99
	–	6.70	0.063	3.04
F	+	6.73	0.075	2.81
	–	8.50	0.061	3.01
FH1	+	6.94*	0.089*	2.61
	–	6.07*	0.090*	2.72
FH2	+	5.14	0.134	2.27
	–	5.90	0.093	2.68
FH3	+	5.32	0.104	2.47
	–	5.96	0.090	2.58
FH4	+	4.58	0.117	2.52
	–	5.86	0.075	2.80
S1	+	4.80	0.081	2.84
	–	6.10	0.055	3.18
S2	+	4.40	0.069	3.01
	–	6.40	0.044	3.34
S3	+	4.67	0.053	3.22
	–	7.33	0.042	3.38
S4	+	4.20	0.149	2.17*
	–	4.45	0.147	2.14*
S5	+	5.34	0.067	2.93
	–	7.20	0.053	3.23
S6	+	5.75	0.086	2.67
	–	6.52	0.075	2.89

**Table 2.** Diversity indices calculated for (a) all plant species, (b) short-lived species, (c) perennials, and (d) mosses in communities with (+) and without (–) *Rhinanthus minor* at three sand dune sites at Holme-next-the-Sea (H1, H2, H3) and one marshland site at Strumpshaw Fen (SF).  $M$ , mean number of species per quadrat;  $C$ , Simpson's Index;  $H'$ , Shannon-Wiener Index. Those pairs of indices for which diversity is higher in the presence of *R. minor* are marked\*

Site	<i>Rhinanthus</i>	Number of species	$M$	$C$	$H'$
a) All plant species					
H1	+	34	5.48	0.086	2.76
	–	32	6.15	0.078	2.84
H2	+	27	5.13	0.089	2.69
	–	28	6.29	0.079	2.78
H3	+	26	5.75	0.092	2.58
	–	34	6.60	0.085	2.74
SF	+	46	7.69	0.060	3.18
	–	48	8.30	0.054	3.24
b) Short-lived species (annuals and biennials)					
H1	+	11	0.51	0.213	1.89*
	–	9	0.73	0.198	1.84*
H2	+	8	0.84	0.224	1.68
	–	10	1.30	0.188	1.85
H3	+	8	0.68	0.477	1.21
	–	11	1.04	0.328	1.60
SF	+	2	0.17*	0.709*	0.47*
	–	2	0.16*	0.781*	0.38*
c) Perennials					
H1	+	23	4.97	0.102	2.50
	–	23	5.42	0.097	2.56
H2	+	19	4.29	0.119	2.36
	–	18	4.99	0.114	2.38
H3	+	18	5.07	0.109	2.35
	–	23	5.56	0.108	2.43
SF	+	44	7.52	0.062	3.13
	–	46	8.14	0.056	3.20
d) Mosses					
H1	+	4	0.62	0.492	0.84
	–	5	0.79	0.412	1.02
H2	+	3	0.36	0.539	0.79
	–	3	0.51	0.405	1.00
H3	+	2	0.22	0.537*	0.66*
	–	2	0.47	0.690*	0.49*
SF	+	7	1.28	0.314	1.34*
	–	6	1.33	0.306	1.32*

data are available the same pattern of species diversity is also found when only the herbaceous perennial component of the flora is considered (Table 2c). Similarly the same pattern emerges, albeit less convincingly, when one considers the annuals and biennials as a single group (Table 2b) and also the mosses (Table 2d). Note though that the number of species on which the diversity indices are based are very low in these cases.

The patterns of diversity reported in Table 2 are those at the time of flowering in *R. minor*. Table 3 shows the diversity of the same communities in the following April, at which time *R. minor* is present in the community only as seedlings. There is again an indication that the pattern of lower diversity in the presence of *R. minor* was present even that early in the season, although it is markedly less

**Table 3.** Diversity indices calculated for each of four communities with (+) and without (-) *Rhinanthus minor* at three sand dune sites at Holme-next-the-Sea (H1, H2, H3) and one marshland site at Strumpshaw Fen (SF) in April 1983, just after the germination of *Rhinanthus minor*. *M*, mean number of species per quadrat; *C*, Simpson's Index; *H'*, Shannon-Wiener Index. Those pairs of indices for which diversity is higher in the presence of *R. minor* are marked\*

Site	<i>Rhinanthus</i>	Number of species	<i>M</i>	<i>C</i>	<i>H'</i>
H1	+	39	6.78	0.054*	3.15
	-	40	6.96	0.054*	3.16
H2	+	29	7.31	0.060*	3.02*
	-	26	8.04	0.064*	2.94*
H3	+	21	5.31	0.100	2.53
	-	28	6.31	0.089	2.68
SF	+	42	6.87	0.066	3.11
	-	42	8.07	0.055	3.26

**Table 4.** The change in diversity indices between April and June for communities with (+) and without (-) *Rhinanthus minor* at three sand dune sites at Holme-next-the-Sea (H1, H2, H3) and one marshland site at Strumpshaw Fen (SF). *M*, mean number of species per quadrat; *C*, Simpson's Index; *H'*, Shannon-Wiener Index

Site	<i>Rhinanthus</i>	<i>M</i>	<i>C</i>	<i>H'</i>
H1	+	+1.30	-0.032	+0.39
	-	+0.81	-0.024	+0.32
H2	+	+2.19	-0.029	+0.33
	-	+1.75	-0.015	+0.16
H3	+	-0.44	+0.008	-0.05
	-	-0.29	+0.004	-0.06
S	+	-0.82	+0.006	-0.07
	-	-0.23	+0.001	+0.02

consistent. The magnitude of the changes in diversity between July and April are given in Table 4. This then represents the recovery from parasitism following the death of *R. minor* in July through to its germination again in the next spring. It can be seen that the diversity at two sites (H1 and H2) increased from July to April, whilst that at sites H3 and SF decreased. Irrespective of the direction of the change, in 10 out of 12 cases the magnitude of the change was greater in the communities which contained *R. minor*.

#### Perturbation experiment

The effects of the removal of *R. minor* on the communities at the four sites in Norfolk were examined in three ways: rank correlation, a contingency  $\chi^2$ , and species diversity indices. A Spearman's rank correlation was performed, for each site, on the species inside and outside the cleared area, with the species ranked according to their frequency in the communities. In all four cases the correlation coefficient was highly significant (Table 5), which indicates that removal of the parasite did not affect the rank abundance of species. The difference in the frequency of each species was then compared at each site by means of a  $2 \times s$  contingency  $\chi^2$  table where *s* is the

**Table 5.** The effects of the removal of *Rhinanthus minor* from the communities at three sand dune sites at Holme-next-the-Sea (H1, H2, H3) and one marshland site at Strumpshaw Fen (SF) on the rank abundance of species as measured by Spearman's rank correlation coefficient ( $r_s$ ) and on the frequency of species in the two communities as measured by contingency  $\chi^2$  (the number of degrees of freedom are given in parentheses). Species responding to the removal of *R. minor* either positively or negatively and which contribute more than 10 to the contingency  $\chi^2$  value are listed. Preferred hosts recorded at that site (##) or another site (#), avoided hosts at that site (††) or another site (†) are also indicated (data from Gibson and Watkinson 1989). No data are available for site SF

Site	$r_s$	$\chi^2$	Species responding to the removal of <i>Rhinanthus minor</i>	
			Positively	Negatively
H1	0.83***	325.0*** (16)	<i>Koeleria macrantha</i> ##	<i>Festuca rubra</i> † <i>Carex arenaria</i> † <i>Elymus farctus</i> †† <i>Bromus hordeaceus</i>
H2	0.72***	220.5*** (110)	<i>Honkenya peploides</i> ## <i>Plantago lanceolata</i> # <i>Leontodon autumnalis</i>	<i>Elymus farctus</i> †† <i>Carex arenaria</i> †† <i>Festuca rubra</i> ††
H3	0.73***	89.5*** (10)	<i>Ononis repens</i> ##	<i>Elymus farctus</i> ††
SF	0.56***	155.9*** (15)	<i>Holcus lanatus</i> <i>Filipendula ulmaria</i>	<i>Carex flacca</i> <i>Carex hostiana</i>

\*\*\*  $P < 0.001$

number of species. Only those species which were sufficiently abundant to have an expected value of greater than 5 were included in this analysis. In every case the value of  $\chi^2$  was highly significant ( $P < 0.001$ ) (Table 5), which indicates that at least a proportion of the species in the community were affected by the removal of *R. minor*. The species which were affected most were those which made the greatest contribution to the overall  $\chi^2$  value; those species which contributed more than an arbitrarily selected value of 10 are listed in Table 5. The removal of *R. minor* had no effect on the number of species at each site but the effect of the removal on Simpson's Index (*C*) and the Shannon-Wiener Index (*H'*) indicated that at three sites (H2, H3 and SF) the diversity was higher in the perturbed areas than in the adjacent unperturbed areas (Table 6). At site H1 diversity was lower in the area from which *R. minor* had been removed.

#### Discussion

*Rhinanthus minor* is usually considered to be a species which is characteristic of species rich grassland (Tansley 1965), but it would appear from the results presented here that it is found in low-diversity patches within these high diversity areas. There are several possible explanations for the pattern that has been observed: (a) *R. minor*

**Table 6.** Diversity indices calculated for communities from which *Rhinanthus minor* had been removed and adjacent communities in which *R. minor* was present at three sand dune sites at Holme-next-the-Sea (H1, H2, H3) and one marshland site at Strumpshaw Fen (SF). *C*, Simpson's Index; *H'*, Shannon-Wiener Index

Site	<i>Rhinanthus</i>	<i>C</i>	<i>H'</i>
H1	Present	0.138	2.33
	Removed	0.193	2.10
H2	Present	0.259	1.62
	Removed	0.221	1.87
H3	Present	0.205	1.86
	Removed	0.193	1.93
SF	Present	0.187	2.06
	Removed	0.184	2.22

might reduce the diversity of the communities in which it grows, by for example preferentially parasitizing and reducing the vigour of non-dominant species; (b) *R. minor* might grow in low-diversity patches, for example by germinating preferentially in these areas; (c) it might be an artifact of the sampling method. An artifact in sampling could arise from the constraints placed upon the locations of the quadrats. The first quadrat of a pair was placed over a *R. minor* plant. This must have been an area of sufficient root density to support the parasite. There were no such constraints on the paired quadrat, which may have encompassed an open area, where root density was too low to permit the survival of *R. minor*. Such open areas frequently contain a number of annual or short-lived perennial species, which would give rise to higher diversity in the quadrats without *R. minor*. The fact that the reduction in diversity in the presence of *R. minor* is present in the perennial component of the vegetation alone might indicate that *R. minor* is altering community structure but it should be noted that the same pattern of diversity is present among the annuals and short-lived perennials (Table 2b), many of which do not appear able to support significant growth of *R. minor*, at least in the greenhouse (Gibson 1986). The same pattern is also present, albeit even less convincingly, if one considers the diversity of mosses (Table 2d), species which certainly cannot support *R. minor*.

The subdivision of the data into various life-history types does not remove the possibility of a sampling artifact completely, although it is suggestive of an effect of the hemiparasite on community structure. Neither can it distinguish between whether *R. minor* reduces diversity, or is merely found in lower-diversity patches. One might predict that if the parasite suppresses diversity, and as it is an annual, the pattern of diversity would be less apparent early in the season, just after germination. Tables 3 and 4 lend some support to this idea in that, whilst the pattern of diversity in the presence of *R. minor* is present even that early in the season, the pattern is markedly less consistent. Certainly the magnitude of the change in diversity is greater in the areas containing *R. minor*, an indication perhaps that *R. minor* has altered the competitive relationship between plants and that there is some readjustment of community structure following the

death of the hemiparasite in July. Nevertheless there is the possibility that the pattern is no more than a "hang-over" from the previous season, as most seeds fall within 50 cm of the parent plant (Gibson 1986).

The most important test of the hypothesis that *R. minor* plays an important role in determining community structure is to examine the effect of the removal of the hemiparasite on species diversity. Following the removal of flowering plants to prevent seed set the net effect of the removal of *R. minor* on the development of the community over the next year was to increase species diversity on three of the sites and decrease it on the fourth (Table 6). Whilst there were no changes in species richness over this period or the rank abundance of species there were significant changes in the abundance of some of the species (Table 5). One would expect those species which responded to the removal of *R. minor* by an increase in abundance to be preferred host species, and those which decreased to be avoided species. Gibson and Watkinson (1989) classified the hosts of *Rhinanthus minor* at Holme-next-the-Sea as preferred or avoided hosts on the basis of the frequency of attachment to each species in relation to the proportion of available roots. If a comparison is made between Table 5 in this paper and Table 5 in Gibson and Watkinson (1989), which shows those species which are selectively parasitized at each of the sites, it can be seen that there is a degree of overlap: *Koeleria macrantha*, *Honkenya peploides* and *Ononis repens* at sites H1, H2 and H3 respectively were preferred hosts and they responded positively to the removal of *R. minor*. *Plantago lanceolata* was also recorded as a preferred host at site H1. Likewise, *Elymus farctus* at sites H1 and H3, and *Festuca rubra* and *Carex arenaria* at site H2 were avoided hosts, and they responded negatively to the perturbation.

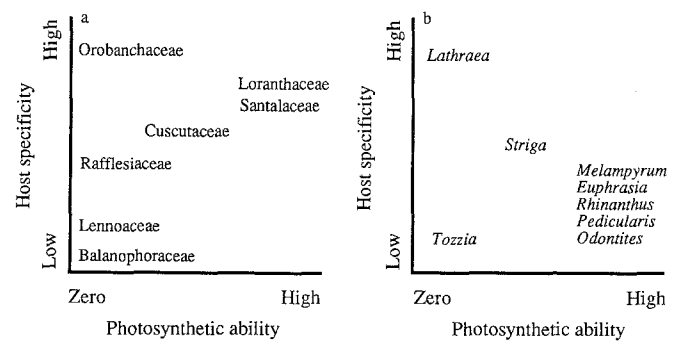
Clearly *Rhinanthus minor*, in certain circumstances, can play a central role in determining the structure of the communities in which it grows. The selectivity of the parasite (Gibson and Watkinson 1989) and the strength of the parasitic interaction is sufficient to modify the competitive relationships between species (Gibson and Watkinson 1991), and have detectable effects on species diversity. Data from the perturbation experiment and from the observational studies indicate that the usual effect of *R. minor* on a community is to suppress species diversity. Site H1 was an exception: the removal of *R. minor* resulted in a reduction in diversity rather than an increase, primarily as result of an increase in the abundance of *Koeleria macrantha*. This is known to be a preferred host (Table 5; Gibson and Watkinson 1989) and the inference from this experiment is that it is also a competitive dominant. The fact that *R. minor* results in a suppression of diversity on most other sites presumably indicates that the preferred hosts on these sites were not competitively dominant. For herbivores it has long been argued (see Harper 1977; Crawley 1983) that selective grazing on what would otherwise be the dominant plant species will inevitably lead to an increase in species diversity by modifying the competitive relationships between the component plant species. Conversely selective feeding on already uncompetitive plants can be expected to

reduce diversity. In the case of *Rhinanthus minor* both effects have been demonstrated, but it would appear that it is usually the less competitive plants that are parasitized. As a consequence the effect of the hemiparasite in vegetation is usually to decrease diversity. The reason for this, and the question of whether it is true of all parasitic plants, remain to be explored.

Intuitively it would seem that a number of basic conditions must be met if a parasitic plant, or indeed any other parasite or pathogen, is to have easily demonstrable effects on the structure of the community in which it grows: (1) the parasite must adversely affect the fitness of its hosts; (2) species within the community must be attacked with different degrees of severity; (3) the host species must constitute a significant part of the community and (4) the parasite must be sufficiently abundant to attack a significant proportion of available hosts. Information relating to the latter two conditions is lacking in the literature, presumably because it is very much dependent on local differences between communities. There is rather more information on the first two conditions.

It might be assumed that the physiological effects of a parasitic plant on its host(s) are directly related to the amount of photosynthate abstracted from the host, which in turn is inversely related to the photosynthetic capacity of the parasite. Therefore, condition (1) can be seen as a continuum from holoparasites to apparently very weak hemiparasites. Likewise condition (2) can be considered a continuum, from those species which utilise only one host species to those which display little or no host selectivity. If these two conditions are represented as axes, it is possible to display the different groups of parasitic plants in two dimensions according to their parasitic behaviour (Fig. 1), and assuming that conditions (3) and (4) are met, one would predict that the effect of the parasite on its community should increase from bottom right to top left with an increase in host specificity and a decrease in photosynthetic ability.

At present there are insufficient data to test this hypothesis. Certainly members of the genus *Orobanche*, which are total parasites, can cause severe reductions in the yield of a range of crops (e.g. Saadi Gharib 1973; Daams 1975; Schmitt 1979; Parker 1986) when they occur at high densities. It is unfortunately not known, however, how the presence of the parasite affects the diversity of the weed flora. Amongst the hemiparasites there are several examples in the Cuscutaceae (Sarpe et al. 1973; Hassawy 1973; Rao and Reddy 1987) and Loranthaceae (Daams 1975) of plants which seriously damage a range of host plants. It has been widely demonstrated that many of these hemiparasites receive a significant proportion of their organic compounds from their hosts (Leonard and Hull 1965; Allred 1966; Salageanu and Fabian-Galan 1968). One might predict that these species would not have the same impact on communities as total parasites with high host specificity, but that they would affect a wider range of communities. Again the data are lacking to test this prediction. Similarly one might predict that hemiparasitic members of the Scrophulariaceae which seem to take little or no photosynthate



**Fig. 1.** **a** The major families of parasitic plants displayed according to their characteristic photosynthetic ability and host specificity (data from Kuijt 1969). **b** Some genera of the Scrophulariaceae classified on the same two axes (based on data in Piehl 1963; Smith 1963; Govier and Harper 1964; Kuijt 1969; Weber 1976; Musselman and Mann 1977). The taxonomic position of *Lathraea* has been the subject of some debate. We follow Clapham et al. (1987) and include the genus in the Scrophulariaceae rather than the Orobanchaceae

from their hosts (Govier et al. 1967; Press et al. 1987) and which generally attack a wide range of hosts (Gibson and Watkinson 1989) would have less of an impact on community structure than hemiparasites in the Cuscutaceae and Loranthaceae. It is nevertheless, as in this paper, members of the Scrophulariaceae that have occasionally been cited as a cause of changes in the species composition of communities (Rabotnov 1959; ter Borg and Bastiaans 1973; Mizianty 1975). Since hemiparasitic Scrophulariaceae primarily extract water and mineral nutrients from their host plants (Smith et al. 1969) one might in particular expect that they would have little effect on their hosts or communities in conditions where neither water nor mineral nutrients are a limiting resource. Certainly the legume *Trifolium repens* is suppressed less by *Rhinanthus minor* in mixtures with *Lolium perenne* when the nitrogen status of the soil is high (Gibson and Watkinson 1991). As varying degrees of host damage can be expected with different levels of water and nutrient availability it would be interesting to add a third axis to Fig. 1 which represented the physiological effects of the diversion of water and nutrients on host fitness so that this too could be related to community structure.

Clearly parasitic plants do have the capacity to play a significant role in determining the structure of the communities in which they occur. This is true even for those species which would appear to be the least likely to have demonstrable effects: those which have a high photosynthetic capability and which attack a wide range of hosts. How frequently this role is actually fulfilled amongst the 3000 species of parasitic flowering plant (Atsatt 1983) is a matter for conjecture, as most work to date has not addressed the subject in this context.

*Acknowledgements.* We should like to thank the Norfolk Naturalist's Trust and the Royal Society for the Protection of Birds for permission to work at Holme-next-the-Sea and Strumpshaw Fen, and NERC for financial support to CCG.

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