

Modelling the growth of parasitic plants

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Summary

1. Hemiparasitic plants, such as *Rhinanthus* species, have substantial effects on community composition and biomass. For example, the presence of parasites often increases diversity but reduces the combined biomass of hosts and parasites by *c.* 25% compared with unparasitized controls. We present and test a simple model of the host–parasite interaction in which parasite growth rate is a function of host growth rate that offers a new explanation for why hemiparasitic plants reduce ecosystem productivity.

2. The model predicts that the combined mass of the host–parasite system is always less than the mass of the host grown alone, because the combined biomass is dependent only on host growth rate, which is reduced by the parasite. The model also predicts that the parasite should adopt an intermediate virulence to maximize its own performance, but that the optimum virulence depends on host growth characteristics.

3. The key assumption of the model is that parasite growth rate and hence parasite biomass is tightly coupled to host growth rate. We tested this assumption by measuring the performance of *Rhinanthus alectorolophus*, a widespread hemiparasitic annual plant, on nine common European grass species. First, we determined size-corrected growth rates for the grasses by fitting power-law growth curves to multiple-harvest data on host individuals grown without *Rhinanthus*. Second, we grew *Rhinanthus* on each of the grass species and related *Rhinanthus* final biomass to the grass species' growth rates.

4. *Rhinanthus* performance was strongly correlated with the growth rate of the host grass species, thus validating a key assumption of our model. However, *Rhinanthus* biomass on three of the nine grass species differed significantly from the value predicted based on host growth rate alone, suggesting that grass species differ in their resistance to parasitism.

5. *Synthesis.* Parameterizing such models of the host–parasite relationship could help to explain variation in *Rhinanthus* performance on different hosts, variation in the effects of hemiparasites in grasslands of different productivity and differences in virulence among parasite populations.

Key-words: coexistence, grassland restoration, hemiparasitic plants, host–parasite interaction, perennial grass species, relative growth rate, *Rhinanthus*, virulence

Introduction

Parasitic plants are one of the largest, most ubiquitous and diverse plant groups, represented by more than 3000 species worldwide and occurring in many different habitats (Press & Graves 1995; Press 1998). In Europe, the most common species are root hemiparasites of the family Orobanchaceae, e.g. *Rhinanthus* species, which occur widely in natural and semi-natural grasslands (Gibson & Watkinson 1989; Matthies & Egli 1999; Joshi, Matthies & Schmid 2000). Such hemiparasites use a wide range of hosts, but their presence has a profound

effect on species composition, suggesting unequal effects on host species (Gibson & Watkinson 1991; Davies *et al.* 1997; Pywell *et al.* 2004, 2007; Bardgett *et al.* 2006; Bullock, Pywell & Walker 2007; Grewell 2008; Niemela, Markkola & Mutikainen 2008). *Rhinanthus* performance also differs depending on host species (Matthies 1996) and some potential hosts have developed resistance (Cameron, Coats & Seel 2006). Hemiparasites can have dramatic effects on the functioning of ecosystems, affecting standing crop, nutrient cycling, decomposition rate and interactions with other trophic levels such as herbivores and pollinators (Marvier 1996; Joshi, Matthies & Schmid 2000; Adler 2002; Phoenix & Press 2005; Press & Phoenix 2005; Quedstedt *et al.* 2005; Bardgett *et al.* 2006; Ameloot *et al.*

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2008). In this study, we present and test a simple model of the host–parasite relationship that helps to explain both individual and system-level effects of hemiparasites.

In contrast to holoparasites, hemiparasites are photosynthetically active, but they rely on the host for water and mineral nutrients, which they extract through specialized structures called haustoria (Seel & Press 1993; Press & Graves 1995; Seel & Jeschke 1999). These structures allow the parasite to access the xylem vessels of the host; for example, Jiang, Jeschke & Hartung (2004) estimated that *Rhinanthus minor* withdraws c. 18% of host nitrogen, 22% of host phosphorus and 20% of host potassium when attached to barley (*Hordeum vulgare*). The removal of nutrients from the host by a hemiparasite clearly compromises host performance (Matthies 1995) and this, coupled with the high densities that hemiparasites can achieve in the field (Westbury 2004), can have dramatic effects on standing crop. Most of the work carried out on hemiparasites in European grasslands has focussed on two closely related species from the genus *Rhinanthus* (*Rhinanthus alectorolophus* and *Rhinanthus minor*). Although these may not be representative of the genus as a whole, we use the word *Rhinanthus* throughout to refer to these two species. A meta-analysis reporting the effect of *Rhinanthus* species (Ameloot, Verheyen & Hermy 2005) showed that the above-ground biomass of host species is reduced by c. 50% in the presence of *Rhinanthus* compared with unparasitized control plots, and that the total combined biomass of hosts and parasites is reduced by c. 25%. The reduction in the combined biomass of host and parasite compared with unparasitized host biomass has been attributed to reduced nitrogen-use efficiency by the parasite compared with the host (Matthies 1995; Ameloot, Verheyen & Hermy 2005) or to reductions in host photosynthesis (Watling & Press 2001; Cameron *et al.* 2008). Here, we use a simple model to provide an additional explanation. If only host plants (but not the parasite) take up resources that limit system productivity, then extraction of resources from the host by the parasite leads to reduced future resource extraction and hence reduced system productivity. In this respect, our model differs from other attempts to model host–parasite interactions that do not generally consider the growth of individuals (Smith *et al.* 2003; Cameron, White & Antonovic 2009).

Our simple model also illustrates how observed differences in parasite performance can be due to differences in host growth rate (faster-growing host species may simply provide more resources to the parasite) or to differences in host resistance (the ease with which *Rhinanthus* can both form and maintain connections may differ depending on host species; Cameron, Coats & Seel 2006; Rümer *et al.* 2007). Some host species are known to be resistant; for example, *Plantago lanceolata* can encapsulate the parasite's invading structures (Cameron, Coats & Seel 2006; Rümer *et al.* 2007) and prevent the removal of host nitrogen (Cameron & Seel 2007); however, grass species are generally considered to be good hosts (Gibson & Watkinson 1991). Nevertheless, the performance of *Rhinan-*

thus has been reported to vary when different grass species were infected (Gibson & Watkinson 1991; Niemela, Markkola & Mutikainen 2008), which could be due to variation in grass growth rates (Grime & Hunt 1975) or to variation in resistance among grasses [grass roots have been observed to lignify root cells in response to contact with *Rhinanthus* haustoria (Rümer *et al.* 2007), although lignification alone does not demonstrate that the host can prevent resource loss (Cameron, Coats & Seel 2006)].

We present a simple model for a host–parasite interaction in which parasite growth rate is a simple function of host growth rate. We use the model to demonstrate that (i) the host–parasite system always exhibits reduced combined yield compared with a host growing alone; (ii) all else being equal, a faster-growing host species will result in a greater final biomass of the parasite; (iii) in most cases, an intermediate level of host resource extraction optimizes parasite performance; and (iv) the optimum level of host resource extraction depends on the type of growth experienced by host plants. We tested the model assumptions by conducting an experiment in which we first determined growth rates for nine host grass species by fitting growth curves to multiple-harvest data on host individuals grown alone (without the parasite). We then measured the performance of the hemiparasitic plant *R. alectorolophus* from different subpopulations and maternal genotypes on the same nine host species and related parasite performance to host growth rates.

Material and methods

A SIMPLE MODEL FOR RHINANTHUS GROWTH

To understand how the growth of the host plant and the parasite might be coupled, it is easiest to start with the very simple case of the growth of a single parasitic plant (e.g. a single *Rhinanthus*) attached to a single host. Although there are a large number of potential formulations for plant growth (Hunt 1982), we chose the power-law growth equation advocated by West, Brown & Enquist (1997, 1999). In this formulation, the instantaneous change in host biomass (M_H) per unit time (t) when growing without the parasite is:

$$\frac{dM_H}{dt} = \beta_H M_H^\alpha, \quad \text{eqn 1}$$

where β_H is a growth coefficient and α is the scaling exponent. This has the following analytical solution:

$$M_{H,t} = \left(M_{H,0}^{1-\alpha} + \beta(1-\alpha)t \right)^{1/(1-\alpha)}, \quad \text{eqn 2}$$

where $M_{H,0}$ is the initial mass of the host and t is the time in days after germination (see also Muller-Landau *et al.* 2006; Russo, Wiser & Coomes 2007). Notice that we have made no explicit assumption about above-ground versus below-ground limitation; we have only assumed that the absolute host growth rate (increase in mass per unit time) is mass-dependent, i.e. that it increases with the biomass of the host plant. We now assume that parasite growth is totally dependent on host growth. This is

presumably always true for holoparasites, but is nearly true for hemiparasites such as *Rhinanthus*, which can barely grow when unattached under nutrient-poor conditions (Matthies 1995). We assume simply that the parasite receives a constant fraction F_R of the host growth:

$$\frac{dM_R}{dt} = F_R \beta_H M_H^\alpha \quad \text{eqn 3}$$

The removal of resources by the parasite causes a reduction in the host growth rate, which is now given by:

$$\frac{dM_H}{dt} = (1 - F_R) \beta_H M_H^\alpha \quad \text{eqn 4}$$

These equations can be solved, giving for the host:

$$M_{H,t} = \left(M_{H,0}^{1-\alpha} + [1 - F_R] \beta_H (1 - \alpha) t \right)^{1/(1-\alpha)} \quad \text{eqn 5}$$

and for the parasite (ignoring the initial mass of the parasite):

$$M_{R,t} = \frac{F_R}{[1 - F_R]} (M_{H,t} - M_{H,0}) \quad \text{eqn 6}$$

Inspection of eqn 5 shows that the final host biomass is higher for: (i) high values of the host growth rate parameter β_H ; (ii) high values of the scaling exponent α and (iii) a lower degree of parasitism (i.e. lower F_R). The final biomass of the parasite is also higher when attached to a fast-growing host (with a high value of β_H and/or a high value of α). However, the final biomass of the parasite has a more complex relationship with the degree of parasitism, with intermediate values of F_R giving higher final parasite biomass (see below).

The model is highly simplified; for example, the fraction of resources removed by the parasite is unlikely to be constant, but we believe that this simple model is sufficient to capture essential features of the system. A more detailed model could include additional complexities, such as the size-dependency of the parasite sink strength relative to the host. We used eqns 5 and 6 to investigate the effect of parasitism on the mass of the host, the mass of the parasite and their combined mass for different values of F and α over the typical 90-day growth period of a hemiparasite such as *Rhinanthus*, assuming biologically realistic parameters ($M_{H,0} = 1$ g and $\beta_H = 0.2$).

ESTIMATING GROWTH RATES OF HOST GRASS SPECIES

The key assumption of the model is that parasite growth rate, and hence parasite final biomass, is tightly coupled to host growth rate. To test this assumption, we selected nine common European perennial grass species as potential hosts for *Rhinanthus*: *Agrostis capillaris*, *Alopecurus pratensis*, *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Bromus erectus*, *Dactylis glomerata*, *Festuca rubra*, *Holcus lanatus* and *Trisetum flavescens* (Lauber & Wagner 2001). Grasses are generally not considered to be resistant to *Rhinanthus*, but they vary greatly in their growth rates, hence we expect highly variable parasite performance due to growth rate differences among grasses. Each grass species was grown under each of three different light regimes (see below) and eqn 2 was fitted to the resulting repeated harvest data allowing estimates of α_i and β_i . To provide a simple comparison of species growth rates unbiased by differences in seed sizes (Turnbull *et al.* 2008; Table 1), we used the parameterized eqn 2 to calculate an absolute growth rate (AGR) at a common reference

Table 1. Seed weight of 100 seeds of the nine experimental grass species

Plant name	Seed weight of 100 seeds (g)
Ag: <i>Agrostis capillaris</i>	0.027
Al: <i>Alopecurus pratensis</i>	0.089
An: <i>Anthoxanthum odoratum</i>	0.053
Ar: <i>Arrhenatherum elatius</i>	0.275
B: <i>Bromus erectus</i>	0.539
D: <i>Dactylis glomerata</i>	0.0102
F: <i>Festuca rubra</i>	0.089
H: <i>Holcus lanatus</i>	0.045
T: <i>Trisetum flavescens</i>	0.028

size, M_c . Similarly, the size-corrected relative growth rate (RGR) (Enquist *et al.* 1999) is then given by

$$\text{RGR} = \frac{1}{M_c} \frac{dM_i}{dt} = \beta_i M_c^{\alpha_i - 1} \quad \text{eqn 7}$$

If – as suggested by West, Brown & Enquist (1997, 1999) – species share a common value of α_i , then differences among species in growth rate at any given common mass are encapsulated by a single parameter, β_i , and the relative ranking of species will be independent of the choice of common size (M_c). If, however, species require different values of α_i , then the relative rankings of species may change depending on the common size chosen. If both AGR and RGR are size-corrected, either can be used to make unbiased comparisons among species (if $M_i = M_c$, then RGR is simply AGR divided by a constant: see eqn 7).

Data collection

From April 2006 individual grass plants were grown from seed for 97 days in a glasshouse in 0.6-L pots containing a mixture of 1 : 1 peat and sand. For each grass species, eight pots were randomly assigned to three light treatments (9 species \times 8 harvests \times 3 light levels \times 3 replicates = 648 plants). Light was manipulated using shade cloths giving three light levels: control (no shade cloth, 100% daylight), 42% daylight and 11% daylight. Seeds of different species were germinated synchronously and were harvested nine times, on days 7, 14, 21, 28, 42, 56, 70, 83 and 97 following germination. Individuals that did not survive were discarded meaning that the number of plants per harvest and per species was between 1 and 3 giving a final total of 629 plants harvested. Plants were irrigated automatically on a daily basis. We measured above-ground plant biomass by clipping the plants at soil level, drying at 80 °C for 48 h and weighing.

The power-law relationship described in eqn 2 can be difficult to fit because of convergence problems if the initial condition ($M_{H,0}$; eqn 2) is included as a free parameter in addition to α_i and β_i . To get convergence, we decided to fix (rather than estimate) the initial biomass of each species on day 0, i.e. germination day, as this can be measured with considerable accuracy. We measured initial seedling size on the day of germination by placing 10 seeds of each grass species on filter paper in a Petri dish. On the day of emergence, the shoot was removed, dried and weighed.

Model fitting

We fitted the model (eqn 2) using generalized nonlinear least squares with the *gnls* function from the *nlme* library (Pinheiro & Bates 2000) for R 2.8.1. (R Development Core Team 2008). Light availability (% daylight) was log-transformed and fitted as a continuous variable.

Because biomass is not log-transformed, initial residuals were strongly heteroscedastic but could be modelled as a power function of time (using the function *varPower*). We used a model-building approach, in which we compared models of increasing complexity, considering models in which both α_i and β_i were functions of light availability and species identity. We identified the most parsimonious model based on minimization of AIC. There was relatively weak evidence for species differences in α_i compared to β_i (see Results). Thus, to compare the influence of increasing model complexity on estimated grass growth rates, we calculated size-corrected AGR (eqn 4) using parameters taken from two different models: (i) AGR_x calculated from a model in which the scaling exponent, α , was light-dependent but common across all species; and (ii) AGR_{x_i} calculated from a model in which the scaling exponent, α_i , was both light-dependent and species-specific. For the model in which α_i was species-specific, relative rankings of species can change depending on the common mass selected and the light level. We investigated this effect by calculating the dependency of AGR_{x_i} on mass and light level within the experimental range.

PERFORMANCE OF *R. ALECTOROLOPHUS* ON DIFFERENT HOST GRASS SPECIES

Data collection

In June 2006, we collected seeds from four individuals of *R. alectorolophus* (*Rhinanthus*) at four sites in semi-natural grasslands around the University of Zurich, Switzerland, giving 16 maternal genotypes in total. The sites were selected because they appeared to differ in the composition and abundance of host species, although this was not quantified. In September 2006, 0.6-L pots filled with the same peat-sand mixture as used for the grass growth experiment were sown with 20 seeds of a single grass species and placed outside in the experimental garden of the University of Zurich (47°23' N, 8°33' E, 546 m a.s.l.). Each of the four maternal genotypes of *Rhinanthus* from each of the four sites was grown on each of the nine host species by sowing nine seeds from a single maternal genotype into each pot at the same time as the grass seed was sown (4 sites \times 4 maternal genotypes \times 9 grass species). In addition, each maternal genotype was grown without a host (4 sites \times 4 maternal genotypes) and each grass species was grown without *Rhinanthus* (9 species \times 2 replicates) for a total of 178 pots. The grass seeds germinated quickly and grew during the mild autumn to form relatively large plants by the following spring. The *Rhinanthus* seeds germinated quite synchronously at the beginning of March, and at this time, we estimated the percentage cover of grass in each pot and harvested all grass hosts growing without *Rhinanthus*. We used the relationship between percentage cover, host species and grass biomass in harvested pots to estimate initial host biomass in the remaining unharvested pots. At the beginning of May 2007, c. 8 weeks after germination of *Rhinanthus* seeds, pots were harvested by clipping all plants at soil level, counting the number of *Rhinanthus* individuals present, drying at 80 °C for 48 h and weighing the biomass of both host and parasite.

Statistical analysis

We first analysed the performance of *Rhinanthus* (final biomass) with linear mixed-effects models (Pinheiro & Bates 2000) using the *lme* function from the *nlme* library for R 2.8.1. The number of *Rhinanthus* individuals and host AGR (eqn 1) were fitted as continuous variables and treated as fixed effects. *Rhinanthus* population (site of provenance) and *Rhinanthus* maternal genotype were treated as nested

random effects. As the variation explained by the random terms was not significant (see Results), the random effects were dropped and we were able to use ordinary least-squares regression. We calculated the AGR of host plant species in four ways using parameters taken from different models under 100% light level and also by assuming either a common initial mass for all species or by incorporating differences in initial mass estimated for each pot (see Data Collection in *R. alectorolophus* section in Materials and Methods). Specifically, using eqn 1, we calculated for each host species: (i) AGR_{xM} estimated from a model with species-specific values of β_i and a single common value of α calculated at a single common size (the estimated average mass of plants in the glasshouse); (ii) AGR_{x_iM} estimated from a model with species-specific values of both α_i and β_i calculated at a single common size (the estimated average mass of plants in the glasshouse); (iii) AGR_{xM_i} estimated from a model with species-specific values of β_i and a single value of α and calculated at a unique mass for each host (the estimated initial host mass for each pot in the garden); (iv) $AGR_{x_iM_i}$ estimated from a model with species-specific values of both α_i and β_i and calculated at a unique mass for each host (the estimated initial host mass for each pot in the garden). We identified the most parsimonious set of parameters by comparing the fit of models based on minimization of AIC.

Results

MODEL BEHAVIOUR

As long as the host growth rate is mass-dependent, the parasite always reduces the total biomass of the system because it reduces the instantaneous host growth rate, an effect that compounds with time. To understand why, it helps to begin with the specific case in which host growth rate is *not* mass-limited (i.e. $\alpha = 0$). In this special case, the combined growth rate of the host and parasite is constant, depending only on the host growth parameter β_i . Therefore, the combined final mass of the host and parasite is insensitive to the degree of parasitism (F_R). But, the fraction of this final biomass that is assigned to the parasite, rather than the host, is set by F_R (Fig. 1a). In this special case, the best solution for the parasite is to extract the maximum possible resources from the host, as resource extraction does not compromise future host growth.

However, mass-independent growth throughout the whole life cycle of a plant is unlikely. Rather, plants usually exhibit an exponential-like phase of growth, during which the growth rate increases with mass. This is captured by our scaling exponent, α . As α increases, host growth is increasingly mass-dependent, such that the reduction in host biomass caused by the resource extraction of the parasite reduces future host growth. In this case, very high resource extraction by the parasite reduces host growth so much that final parasite biomass is strongly compromised. However, very low resource extraction also leads to low final parasite biomass, simply because the parasite has taken so few resources from the host. Hence, the optimum resource extraction level by the parasite is intermediate (Fig. 1b). As the value of α increases – that is, as host biomass becomes increasingly mass-limited – the effect of resource extraction by the parasite on host mass and the combined mass of the system becomes more dramatic, and parasite performance is more severely compromised at high extraction rates. With our chosen parameters ($M_{H,0} = 1$ and $\beta_H = 0.2$), the optimum fraction

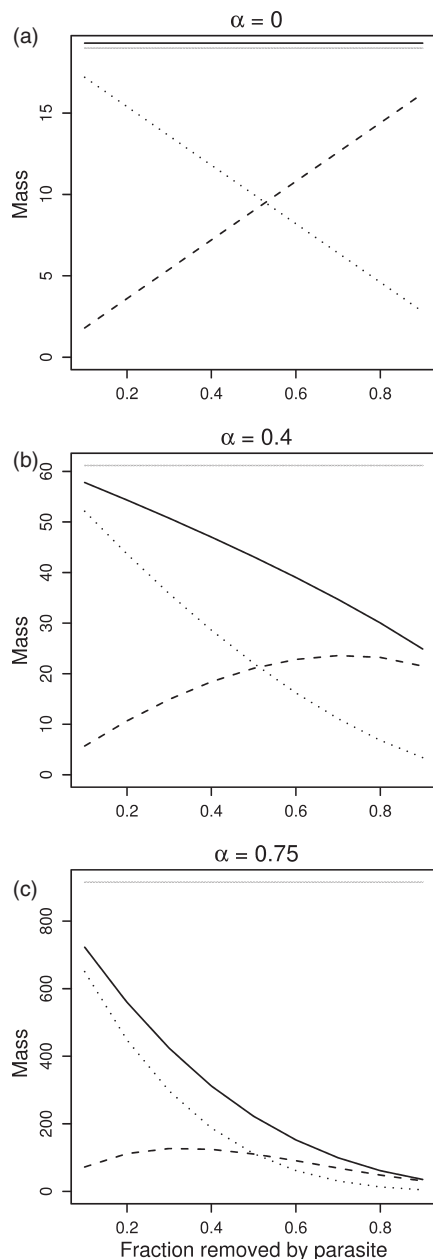


Fig. 1. Results of a host–parasite model in which the host grows according to a power law with a scaling exponent (α) and the parasite removes a constant fraction (F_R) of the host growth rate. The host mass when grown alone (grey, solid), the host mass when grown with the parasite (dotted) and the parasite mass (dashed), together with their combined mass (black solid) are shown. Note the different range on the y-axes in (a–c). In (a) the grey line has been shifted down for clarity.

of host resources to remove when $\alpha = 0.4$ is $F_R \sim 0.7$, whereas when $\alpha = 0.75$, the optimum fraction of host resources to remove is only $F_R \sim 0.3$ (Fig. 1b,c).

ESTIMATING GROWTH RATES OF HOST GRASS SPECIES

There was strong evidence that both the allometric constant β and the scaling exponent α were light-dependent

($F_{1,609} = 49536.2$, $P < 0.001$ and $F_{1,609} = 44.2$, $P < 0.001$, for β and α , respectively) and varied among host species ($F_{8,609} = 1063.1$, $P < 0.001$ and $F_{8,609} = 5.6$, $P < 0.001$, for β and α , respectively). However, although the best fit was obtained for the model in which α was both light-dependent and species-specific, the additional complexity made only limited changes to the fitted curves compared, for example, with models in which α varied with light level but not with species (Fig. 2). When not allowed to vary among species and light treatments, the best estimate of the scaling exponent is $\alpha = 0.857$ (SE = 0.004). When light-dependent, the value of α increases with increasing light availability (slope = 0.048), thus giving under 11% light, $\alpha = 0.833$, under 42% light, $\alpha = 0.861$ and under 100% light, $\alpha = 0.879$. When light-dependent and species-specific, α_i varied in the range 0.782–0.904 (Table 2).

When using parameters from the most complex model (in which both α_i and β_i are species-specific), there were changes in the rankings of species' growth rates with both mass (M_c) and light (Fig. 3). Species' rankings can change with mass because the value of α_i determines how quickly growth slows with increasing mass; for example, *B. erectus* has the lowest value of α_i in our data set and therefore its growth rate declines more rapidly with size when compared with other species (Fig. 3a). Similarly, there is an imperfect correlation between species growth rates in different light levels (Fig. 3b). However, the change in rankings of species' growth rates was rather limited, and there was certainly no evidence that species with the highest growth rates in low light have the lowest growth rates in high light (Sack & Grubb 2001; Kitajima & Bolker 2003).

PERFORMANCE OF *R. ALECTOROLOPHUS* ON DIFFERENT HOST GRASS SPECIES

Rhinanthus individuals grown without hosts had an average biomass of only 0.037 g (SD = 0.014) compared with an average mass of 0.297 g (SD = 0.145) when grown with a grass host (a c. 8-fold difference), suggesting that under these conditions, *Rhinanthus* growth is strongly dependent on host growth. Of the four different estimates of host AGR, the best predictor of *Rhinanthus* biomass was that calculated using the simplest model, with a common scaling exponent α shared among species and where species are assumed to have the same initial mass (AIC = −191.4, $AGR_{\alpha M}$; Fig. 4a). AGR calculated in this way was a substantially better predictor than any of the three more complex alternatives ($AGR_{\alpha_i M}$ AIC = −180.1, $AGR_{\alpha_i M_i}$ AIC = −159.9 and $AGR_{\alpha_i M_i}$ AIC = −160.0; Fig. 4). Using the calculation of host AGR from the simplest model, differences in host growth rate are determined only by the species-specific allometric constant β_i . A substantial part of the variation in the performance of *Rhinanthus* was explained by this positive linear effect of grass growth rate (slope with 95% CI = 2.8 (1.8–3.8), $R^2 = 0.34$; Fig. 3). There was no significant variation around this slope between the provenance of *Rhinanthus* mother plants (likelihood ratio test: $\chi^2 = 1.1$, $P = 0.29$) or across *Rhinanthus* maternal genotypes ($\chi^2 = 0.6$, $P = 0.48$). When using the

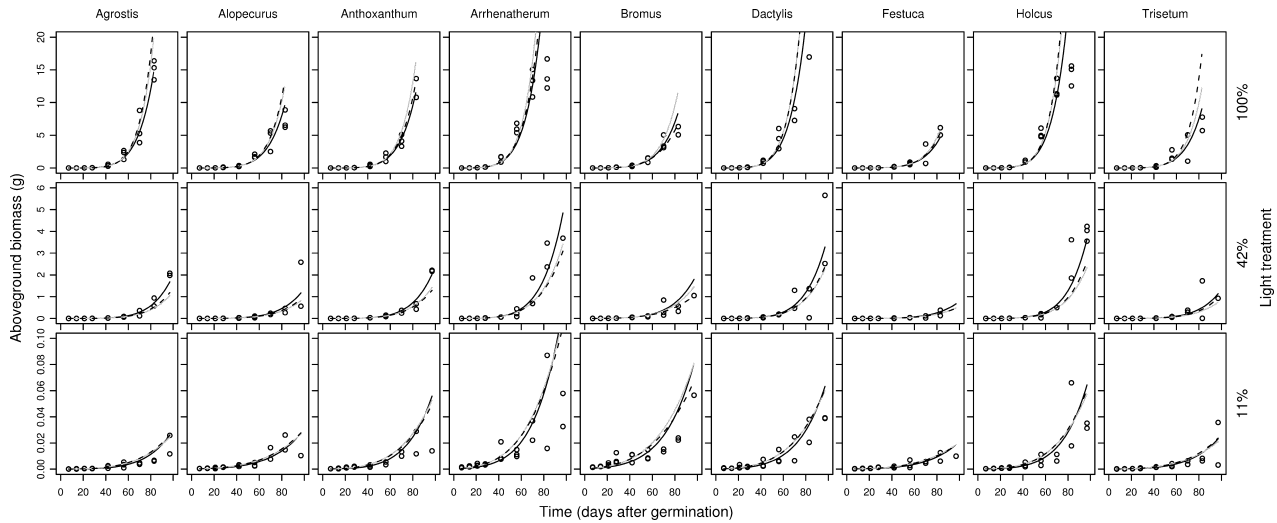


Fig. 2. Fitted growth rate curves for nine common perennial grass species grown under three light levels (upper panel: 100% daylight; middle panel: 42% daylight; and lower panel: 11% daylight). The growth rates are from fitted models with a single common value of α (black, solid), with α light-dependent but not species-specific (grey, solid) or with α both light-dependent and species-specific (dashed). Note decreasing range of biomass (y -axis) going from the top to bottom row.

Table 2. Average biomass M and parameter estimates (α and β ; eqn 1) from different growth models

Light treatment (%)	Species	$\beta_{i,\alpha}$	β_{i,α_i}	β_{i,α_i}	α	α_i	α_i	M (g)
100	<i>Agrostis capillaris</i>	0.106	0.116	0.120		0.879	0.887	
	<i>Alopecurus pratensis</i>	0.093	0.101	0.103			0.886	
	<i>Anthoxanthum odoratum</i>	0.099	0.110	0.103			0.864	
	<i>Arrhenatherum elatius</i>	0.113	0.122	0.116			0.861	
	<i>Bromus erectus</i>	0.088	0.096	0.079			0.825	
	<i>Dactylis glomerata</i>	0.112	0.122	0.122			0.880	
	<i>Festuca nigrescens</i>	0.083	0.092	0.089			0.872	
	<i>Holcus lanatus</i>	0.116	0.127	0.129			0.886	
	<i>Trisetum flavescens</i>	0.095	0.105	0.116			0.904	
42	<i>Agrostis capillaris</i>	0.062	0.053	0.056	0.857	0.837	0.849	2.325
	<i>Alopecurus pratensis</i>	0.053	0.046	0.049			0.847	
	<i>Anthoxanthum odoratum</i>	0.062	0.054	0.051			0.825	
	<i>Arrhenatherum elatius</i>	0.068	0.061	0.058			0.823	
	<i>Bromus erectus</i>	0.055	0.050	0.040			0.786	
	<i>Dactylis glomerata</i>	0.065	0.057	0.059			0.841	
	<i>Festuca nigrescens</i>	0.049	0.043	0.042			0.834	
	<i>Holcus lanatus</i>	0.069	0.060	0.063			0.847	
	<i>Trisetum flavescens</i>	0.056	0.047	0.056			0.865	
11	<i>Agrostis capillaris</i>	0.027	0.015	0.018		0.772	0.789	
	<i>Alopecurus pratensis</i>	0.023	0.014	0.015			0.788	
	<i>Anthoxanthum odoratum</i>	0.030	0.018	0.017			0.766	
	<i>Arrhenatherum elatius</i>	0.031	0.021	0.020			0.763	
	<i>Bromus erectus</i>	0.027	0.018	0.014			0.726	
	<i>Dactylis glomerata</i>	0.028	0.018	0.019			0.781	
	<i>Festuca nigrescens</i>	0.022	0.013	0.013			0.774	
	<i>Holcus lanatus</i>	0.031	0.019	0.021			0.788	
	<i>Trisetum flavescens</i>	0.024	0.014	0.018			0.806	

$\beta_{i,\alpha}$ are the values estimated from a model with a single common value of α among species and light treatments. β_{i,α_i} are the values estimated from a model where α_i is light-dependent but not species-specific. β_{i,α_i} are the values estimated from a model where α_i is both light-dependent and species-specific. M is the estimated average mass of plants in the glasshouse.

best model (AGR _{αM}), there was still significant variation among grass host species in *Rhinanthus* performance after differences in host growth rate had been taken into account

(likelihood ratio test: $\chi^2 = 6.2$, $P < 0.001$, $R^2 = 0.45$), i.e. host grass species remained significant when fitted after the host grass growth rate. In particular, *Rhinanthus* had a

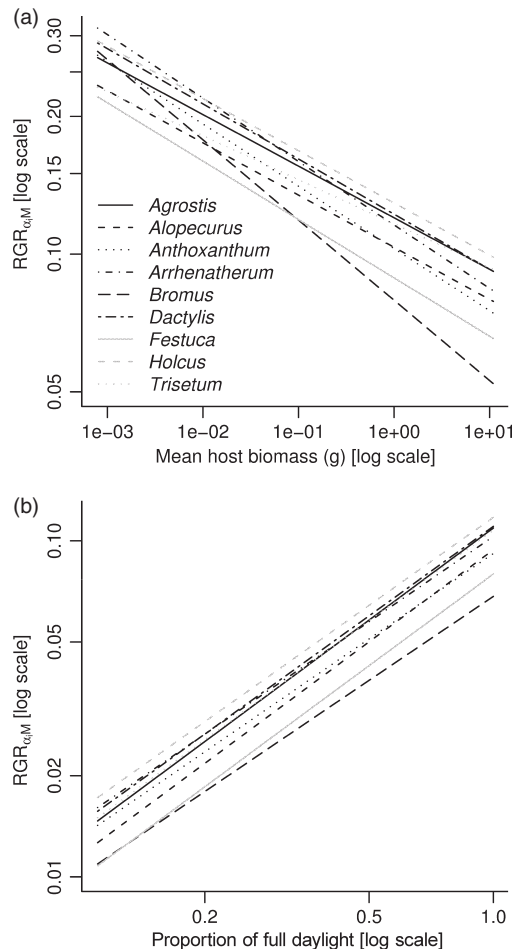


Fig. 3. Relationship between the size-corrected relative growth rate (RGR) of the host (grown without the parasite) and (a) host biomass, and (b) light availability. RGR was estimated at a common size (eqn 6) using parameters from models in which α_i and β_i are light-dependent and species-specific. For (a), the common size (mean host biomass) ranges from the average initial mass of plants in the glasshouse to the average final mass of plants in the glasshouse. For (b), RGR was calculated at a single common size (the average mass of plants in the glasshouse).

substantially lower performance than expected when grown with *Anthoxanthum odoratum* and *H. lanatus* and a substantially higher performance than expected when grown with *D. glomerata* (Fig. 4a).

Discussion

Our simple model assumes that the host plant actively takes up limiting nutrients and the parasite steals some fraction of this uptake; but, in doing so, it reduces the host growth rate and hence further nutrient uptake. Thus, as is commonly observed, the combined mass of the host–parasite system is always lower than the mass of the host growing alone. We believe that this mechanism could contribute to the observed reduction in yield in plant communities infected with parasitic plants, although previous explanations for this effect – reductions in host photosynthesis (Cameron *et al.* 2008), inefficient nutrient use by parasites compared with hosts (Matthies 1995) and a shift in

species composition towards species with lower growth rates (Bardgett *et al.* 2006) – undoubtedly also play some part. Comparison of the relative contributions of these alternative mechanisms is a goal for future research.

Our simple model shows that an intermediate level of resource extraction maximizes individual parasite yield. Thus, an ‘ideal’ parasite would exercise prudent, rather than maximum, resource extraction. Variation in virulence among populations of *Rhinanthus* has been documented (Mutikainen *et al.* 2000), although a comprehensive study is lacking. The optimum virulence depends strongly on the host growth characteristics, but might also depend on the degree to which different individuals of the parasitic plants compete with each other, e.g. when multiple *Rhinanthus* individuals are attached to a single host plant, as is commonly observed (Prati, Matthies & Schmid 1997; Westbury 2004). Competition among parasites selects for higher virulence because a prudent parasite no longer benefits from the under-utilization of the host (Frank 1996). Therefore, according to our model, the result of competition between parasitic plants would be (i) a reduction in the final, combined mass of the multiple parasitic plants, compared with the final mass of a single parasite; and (ii) an even greater reduction in the final biomass of the whole system (hosts plus parasites).

Although it is often reported in the literature that *Rhinanthus* infects fast-growing grasses as preferred hosts (Ameloot, Hermý & Verheyen 2006; Bardgett *et al.* 2006), no previous study has tried to relate the performance of the parasite to the growth rate of the hosts. We found that *Rhinanthus* performance was strongly correlated with the growth rate of the host grass species, thus validating a key assumption of our model; however, *Rhinanthus* biomass on three of the nine grass species differed significantly from the predicted value, suggesting that grasses may differ in their resistance to parasitism. Although Cameron, Coats & Seel (2006) have demonstrated substantial resistance in forbs, lignification of infected grass roots suggests that some grass species may also exhibit partial resistance (Rümer *et al.* 2007). However, it is also possible that the deviations in the performance of *Rhinanthus* on these three species may be due to differences in the growth rates of host grasses inside the glasshouse compared with outside in the garden.

GROWTH RATES OF HOST GRASS SPECIES

Conventional measures of RGR are usually an average calculated over some common time interval. However, as the instantaneous growth rate expressed by an individual plant declines as it grows (Grime & Hunt 1975; Hunt 1982; Enquist *et al.* 1999), average growth rates measured in the usual way are heavily biased by initial size (Turnbull *et al.* 2008) and this bias could potentially mask important trade-offs, e.g. between growth rates in high versus low light levels (Kitajima & Bolker 2003; Sack & Grubb 2003). We found that the rankings of species in terms of growth rate changed with light availability, although only to a limited degree, suggesting that such a trade-off is perhaps of limited importance. Surprisingly, there were more substantial crossovers in species growth-rate ranks with

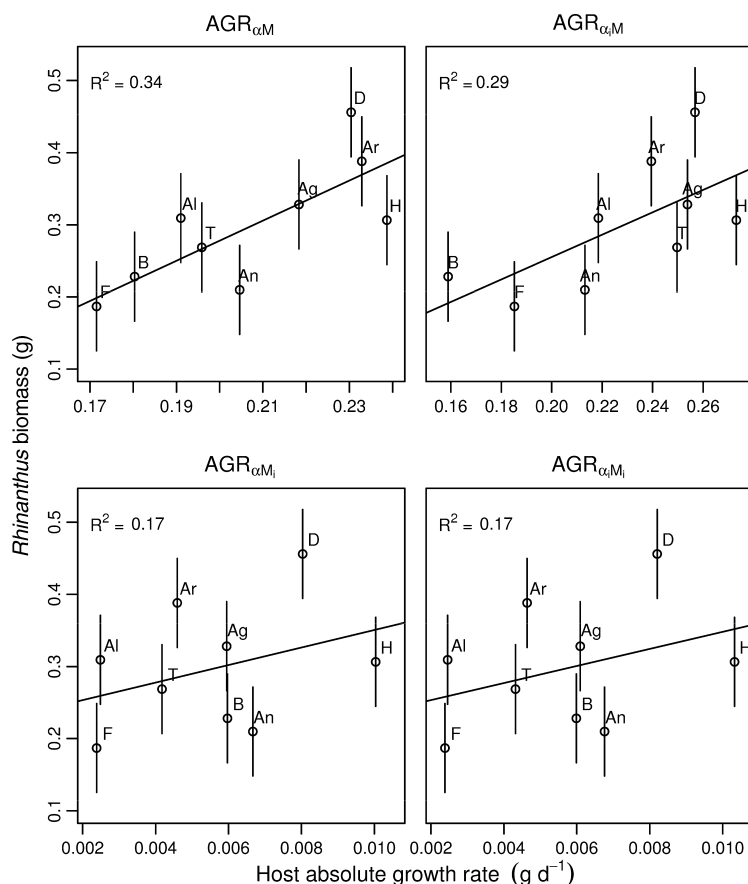


Fig. 4. Relationship between the final biomass of *Rhinanthus* and the absolute growth rate (AGR) of nine common perennial host grass species (grown without the parasite). The different values of AGR are calculated using models of increasing complexity, see text for details of AGR calculations. Ag = *Agrostis capillaris*, Al = *Alopecurus pratensis*, An = *Anthoxanthum odoratum*, Ar = *Arrhenatherum elatius*, B = *Bromus erectus*, D = *Dactylis glomerata*, F = *Festuca rubra* ssp. *commutata*, H = *Holcus lanatus* and T = *Trisetum flavescens*. Means \pm 95% confidence intervals are shown. Note that the scale of the host AGR (x-axis) is smaller on the two lowest panels because the estimated initial host mass in the garden was much smaller than the average mass in the glasshouse.

increasing mass, although the relevance of this for coexistence is unclear.

The network model of West, Brown & Enquist (1997, 1999, WBE model) predicts that the growth rate declines with plant mass to the 3/4; power for most plants ($\alpha = 0.75$) with the exception of seedlings ($\alpha \approx 1$). When fitting these models to individual grass plants, we found that the best estimate of the common scaling exponent under 100% light was $\alpha = 0.879$ (95% CI = 0.871–0.888), and in the species-specific model, α_i ranged from 0.825 (95% CI = 0.790–0.860) to 0.904 (95% CI = 0.882–0.926). Grasses were grown from seed (and hence presumably could be classified as seedlings for some initial period) and this might explain why the measured values of α are higher than expected; however, the value of α also increases with increasing light. This is despite the fact that plants were much smaller in the low-light treatment and hence could presumably be classified as seedlings for longer. The growth of individual grass plants was also best described by a model in which α_i was species-specific, suggesting that the growth rates of different species (even those belonging to the same life-form) scale differently with mass.

PERFORMANCE OF *R. ALECTOROLOPHUS* ON DIFFERENT HOST GRASS SPECIES

The best predictor of *Rhinanthus* performance was absolute host growth rate calculated from a relatively simple model with a common scaling exponent α and by ignoring variation in the

initial mass of the hosts. One possibility is that the initial growth rate model was overfitted, and this is a known danger when using the AIC for model selection (Anderson 2007). Overfitting implies that some noise (non-information) has been included in the structural part of the model and the effects are not part of the actual process under study. Hence, including too many parameters makes the model so specific to the particular data set that prediction for new data sets is unreliable (Anderson 2007). That the best predictor of *Rhinanthus* performance came from a model ignoring variation in initial host mass could alternatively be due to a difference in the nature of host growth between the glasshouse and the garden. In the glasshouse, single plants were grown in large pots, and there was little evidence of resource restriction; however in the garden multiple grass seeds were sown. These seeds germinated quickly and grew during the autumn to form a dense sward, and by early spring, plants already filled the pots. It is therefore possible that, due to resource restriction, growth was no longer limited by above-ground mass. In this case the exponent in eqn 1, α , might fall to 0, and the growth rate is given simply by β_i . For example, Turnbull *et al.* (2008) found that a model with a switch from exponential to linear adequately captured the growth of annual plants grown in small restricted pots.

Conclusions

We developed a simple model for the growth of a host plant coupled to a parasite (or hemiparasite) and tested a key

assumption of this model. The model predicts that (i) the combined mass of the host–parasite system is always less than the mass of the host grown alone simply because, by removing host resources, the parasite reduces future resource uptake; (ii) final parasite biomass should be greater when the parasite is growing on host species with higher growth rates; and (iii) *Rhinanthus* should adopt an intermediate virulence to maximize its own performance, although competition among parasites should select for increased virulence. All the grass species tested made good hosts for the parasite, and the major differences in parasite performance were explained by variation in host growth rates; however, there was evidence for some differences in resistance among host grass species. We conclude that extending and parameterizing this model for different *Rhinanthus* populations could help to explain the variation in the effect of the parasite in different grasslands, for example grasslands differing in productivity.

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