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Exploitative competition between two seed parasites on the common sedge, *Carex nigra*

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We present results from a two-year experiment studying the competitive interaction between the gall mite *Phytoptus caricis* and the smut fungus *Anthracoidea heterospora*. A factorial addition/removal experiment showed that a negative interaction occurs between *A. heterospora* and *P. caricis*, presumably due to competitive interactions in the early infection process of their shared resource, developing utricles on the common sedge, *C. nigra*. Strong effects of interspecific competition for both species were only evident in 1995 while *A. heterospora* showed some signs of suffering negative effects from competition also in 1994. Results thus suggest that significant effects of competitive interaction may only be apparent when densities of the two competitors are fairly high. The interaction was strongly asymmetric, with *A. heterospora* being more affected by the presence of *P. caricis* than vice versa. Estimates of interaction strength for *A. heterospora* were about twice as large compared to that for *P. caricis*. The difference in interaction was significant when data were pooled over the two years of the study. The study highlights the need to consider interspecific interactions between different plant parasites when studying the effects of plant pathogens.

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The importance of interspecific interactions in shaping the distribution patterns of various plant parasites has received much attention in the literature. The majority of the published studies have focused on competition between different phytophagous insects (see Denno et al. 1995, for a review), while surprisingly few have turned the attention to other plant parasites, such as pathogenic fungi, bacteria and viruses. The lack of attention does not, however, indicate that pathogens are of minor importance in natural populations and over the last decade population biologists have started to acknowledge the dramatic effects that pathogens can have in natural populations (Alexander 1992, Gilbert and Hubbell 1996).

The conclusions drawn from the studies on interspecific competition among plant parasites (primarily phytophagous insects) are somewhat ambiguous, with some experiments identifying competition as a major force in structuring communities of plant parasites, while other experiments have failed to detect any evidence for competition being important in natural populations (Schoener 1983, Denno et al. 1995).

Interactions between different plant parasites are often manifested through some form of exploitation competition (Schoener 1983, Denno et al. 1995), although interference competition also appears to be a common form of competition among certain guilds of phytophagous insects (Denno et al. 1995). A common example of exploitation competition is that host tissue devoured by one animal is clearly not available for exploitation by other parasites (see for instance Bowers and Sacchi 1991, Hatcher et al. 1994, Ericson and Wennström 1997, Hudson and Stilling 1997). A similar logic applies to host tissue infected by a pathogen that

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might be rendered unsuitable as a food source for many phytophagous insects (Karban et al. 1987).

The gall mite *Phytoptus caricis* and the smut fungus *Anthracoidea heterospora* both infect developing utricles of their common host plant, the sedge *Carex nigra*. Individual utricles can be infected by either *A. heterospora* or *P. caricis* but they never develop symptoms of the other parasite. Moreover, only rarely will they be found infecting utricles on the same inflorescence of an individual host plant (PKI pers. obs). However, different inflorescences on the same tussock will readily be infected by either *A. heterospora* or *P. caricis* (Ingvarsson and Ericson 1998). In an earlier large-scale survey of the abundance of both *A. heterospora* and *P. caricis* in several *C. nigra* populations, we found a strong negative association between levels of infection of the two parasites in years when parasite abundance were high (Ingvarsson and Ericson 1998). We thus speculated that some form of negative interference between the two parasite species was responsible for their repulsed distribution (Ingvarsson and Ericson 1998). However, while a pattern of negative association between the distribution of two potentially competing species has often been used as evidence for interspecific competition (e.g. Schoener 1974, McLain 1981), several studies have failed to detect competition between pairs of species even though they show a negative association in the field (Karban 1987, Denno et al. 1995). Some studies have even suggested that species which respond similarly to host plant variation could show positive association despite fairly intense competition (Fritz et al. 1987, Denno et al. 1995). Thus, inferring competition on the basis of observed negative associations in natural populations is clearly not satisfactory and carefully designed experiments are needed to establish clear evidence for negative interactions between pairs of species (Schluter 1984, Hastings 1987).

Therefore, to investigate the potential interactions between *A. heterospora* and *P. caricis* in more detail we performed a factorial removal/addition experiment to determine whether there was any evidence for negative interactions between *A. heterospora* and *P. caricis*. Our a priori expectation was that if the two parasite species were competing for a shared resource (i.e. the developing utricles on the host plant), the presence or absence of the potential competitor should influence the observed levels of the focal parasite. We were also interested in determining interaction strengths between the two species. Exploitation competition is often highly asymmetric, with one species often suffering more severe effects due to competition (Denno et al. 1995). *P. caricis* and *A. heterospora* differ in their timing of infection, with *P. caricis* infecting the developing utricles very early in the season while *A. heterospora* infection usually takes place one to two weeks later, during or right after anthesis (Ingvarsson and Ericson 1998). These differences in the timing of infection should result in *P. caricis* having large quantities of suitable host tissue available at the time of infection, while *A. heterospora* may be limited to inflorescences not already infected by *P. caricis*. We therefore expected the interactions between *P. caricis* and *A. heterospora* to be asymmetric, with *P. caricis* exerting a stronger effect on *A. heterospora* than vice versa.

Material and methods

Study organisms

Carex nigra L. (Cyperaceae) is a common sedge in moist–wet mire vegetation types and along shores throughout Fennoscandia. *C. nigra* is a polymorphic taxon and along the eastern coast of Sweden it is mainly represented by the variety *recta* Hyl. This variety forms dense tussocks that occur as discrete, easily identified patches on the shores. *C. nigra* is primarily selfing and seed set is close to 100%. Infection by either *A. heterospora* or *P. caricis* renders utricles completely sterile and the parasites can therefore have severe impact on the seed set of the host plant.

Anthracoidea heterospora (B. Lindb. ap. Nannf. & Lindb.) Kukk. (Ustilaginales) is a non-systemic ovaricolous smut that infects most species of *Carex* sect. *acutae* and is common on *C. nigra* (Kukkonen 1965, Kukkonen and Vatanen 1968). Detailed descriptions of the biology of the smut can be found in Lehtola (1940), Nannfeldt and Lindberg (1965) and Nannfeldt (1979). Teliospores germinate in early summer, releasing basidiospores which subsequently infect florets of the host plants during anthesis (Kukkonen and Vatanen 1968). Infection may also take place by vegetatively produced conidia of the imperfect *Crotalia* stage. Successful infection results in the replacement of the utricle by a smut sorus, first gray in color due to a coating of sterile hyphae, then black when spores mature. After the growth period the sori usually remain attached to the inflorescence. The floral shoots wilt down during autumn and early winter and the compact mass of spores stays intact, and can be found in the litter at the base of each tussock the following spring. Disease incidence and severity vary strongly between taxa, sites and years (Nannfeldt 1979, Ingvarsson and Ericson 1998). It has been generally assumed that basidiospores are wind-dispersed; however, recent studies have shown that beetles of the species *Phalacrus substriatus* are primarily responsible for transmission, at least within single populations of the host plant and that high disease levels are correlated with the presence of the beetle (Ericson et al. 1993, Ingvarsson and Ericson 1998).

Phytoptus caricis (Acari; Eriophytidae) (Lehtola 1940), is a gall mite that oviposits in the developing utricles of *C. nigra*. This gall-forming mite is only known to infect *C. nigra*. Infested utricles are easily

recognized as they are elongated (at least twice the length of healthy utricles) and that the perigynium change color from green to first yellowish-brown and later violet-brown (Lehtola 1940). The mites overwinter inside the utricles, at the base of the *C. nigra* tussock. In early summer they infect female flowers early during anthesis when females oviposit a single egg within a developing utricle.

Experimental design

This study was performed in the Skeppsvik area, Sävar parish, 20 km E of Umeå, Sweden. In September 1993 we collected inflorescences that were heavily diseased by *A. heterospora* or *P. caricis* from a number of *C. nigra* populations. During the first week of October 1993 we selected three sites along the coastline surrounding the Skeppsvik archipelago where *C. nigra* occurs abundantly. These sites were separated from each other by 1–3 km (Fig. 1).

These sites were selected since they had been free of *A. heterospora* disease for at least two consecutive years before the experimental start in October 1993 (Ingvarsson and Ericson unpubl.). At site 1, *A. heterospora* was found in the vicinity of the experimental population but not on any of the experimental tussocks. The nearest *A. heterospora* diseased *C. nigra* tussocks was found approximately 70 m away from the experimental site. At site 2 and 3 the closest diseased tussocks were 160 m and 300 m away, respectively. We took the precaution of using only disease free localities since teliospores of *A. heterospora* have been found to survive for more than one year under field conditions (Ericson pers. obs). Inflorescences infected by *P. caricis* were found within the experimental populations at all three sites, but gall incidence were relatively low (incidence 5–10%). In October 1993 we removed, by hand, all inflorescences infected by *P. caricis* from all tussocks in the experimental area at all three sites. At this time the floral shoots were still erect and the infected utricles remained attached to the floral shoots.

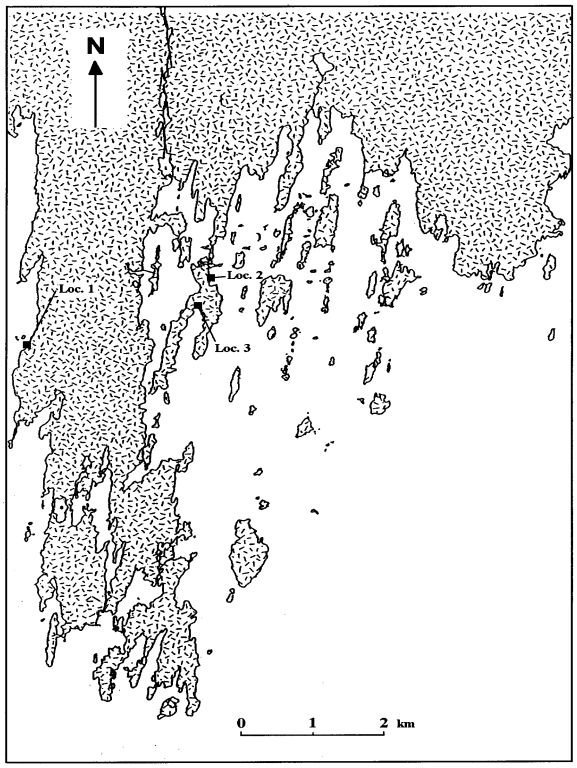

Fig. 1. Map of Skeppsvik Archipelago, northern Sweden, showing the location of the three study sites.

At each site, we haphazardly selected 20 tussocks of *C. nigra* to be included in the experiment. The distance between experimental tussocks were 3–5 m. Each of the 20 tussocks were assigned to one of four different treatments; 1) control tussocks ($A-/P-$), 2) *A. heterospora* and *P. substriatus* present ($A+/P-$), 3) *P. caricis* present ($A-/P+$) and 4) both *A. heterospora*, *P. substriatus* and *P. caricis* present ($A+/P+$). In October 1993, we placed five inflorescences that were heavily infested by *P. caricis* at the base of the *C. nigra* tussocks belonging to treatment $A-/P+$ or $A+/P+$. These *P. caricis* infected inflorescences had all been collected from several populations in the Skeppsvik area in September and October 1993 and been stored outdoors in paper-bags before the experiment. The experimental sites were revisited early in June 1994 and we then placed five inflorescences heavily diseased by *A. heterospora* in all tussocks belonging to treatments $A+/P-$ and $A+/P+$. In these tussocks we also placed two pairs of *P. substriatus* beetles that had been collected from a population ca 20 km south of Skeppsvik a week earlier. *P. substriatus* beetles act as vectors of *A. heterospora* and addition of the beetles was done to ascertain successful inoculation of the fungus (cf. Ericson et al. 1993).

The experimental sites were then revisited in early August to record the disease levels of *A. heterospora* disease and gall abundance of *P. caricis*. We counted the number of smutted or gall infested utricles on all experimental tussocks. Disease level and gall abundance was scored as the number of smutted or galled utricles divided by the number of inflorescences on the tussock. It was possible to standardize parasite abundance in this way since there was very little variation in number of seeds per inflorescence, both among floral shoots on a tussock and among tussocks. The experimental populations were visited again in August 1995 and disease levels and gall abundance were scored in the same manner as in 1994.

Table 1. Abundance of *A. heterospora* and *P. caricis* for the three experimental sites in 1994 and 1995. Data is combined over all treatments. Standard errors are shown in parentheses.

	1994		1995	
Site	*A. heterospora*	*P. caricis*	*A. heterospora*	*P. caricis*
1	0.111 (0.022)	0.347 (0.053)	0.181 (0.037)	0.417 (0.060)
2	0.011 (0.009)	0.051 (0.035)	0.163 (0.043)	0.368 (0.050)
3	0.163 (0.023)	0.278 (0.043)	0.265 (0.046)	0.349 (0.060)

Statistical analysis

We analyzed the data from the experiment using a mixed-model ANCOVA. The treatments are presence/absence of *A. heterospora*/*P. substriatus* ($A+$ or $A-$), presence/absence of *P. caricis* ($P+$ or $P-$). We also included experimental site (S) in the statistical model. Tussock size, measured as the number of flowering shoots, was used as a covariate to correct for any variation in parasite abundance that may arise from variation in tussock size. Both presence/absence of *A. heterospora* and *P. caricis* (A) and (P) were considered fixed effects, while site (S) was considered a random effect. Since we only could manage to survey three sites (due to logistical problems) we analyzed the model with the treatments nested within sites, as suggested by McKone and Lively (1993; see also Shen 1995). While this method of analysis will reduce our ability to generalize across sites and also prevents us from testing whether treatment effects differ between sites, we still chose this model to increase our statistical power in detecting treatment effects with a given site (McKone and Lively 1993, Lively and McKone 1994).

The interesting term in the statistical model is the interaction term $A \times P$. A significant $A \times P$ interaction indicates that the effects of either treatment (A or P) depended on the presence/absence of the other species (P and A, respectively). To be more precise, if the $A \times P$ interaction term turned out to be significant, we proceeded to specifically test whether the presence of the presumed competitor species resulted in lower levels of infection target species. The analyses were performed on disease severity of both *A. heterospora* and *P. caricis*, for data from both 1994 and 1995. We performed the analysis using both untransformed and arcsine square root transformed data. The two analyses gave virtually identical results and we therefore only present results based on the analysis carried out using untransformed data. All statistical analyses were made using the statistical software package Systat.

Estimating interaction strength

To determine whether the competitive effects were asymmetric between the two species we used the experimental data to calculate the interaction strengths. In-

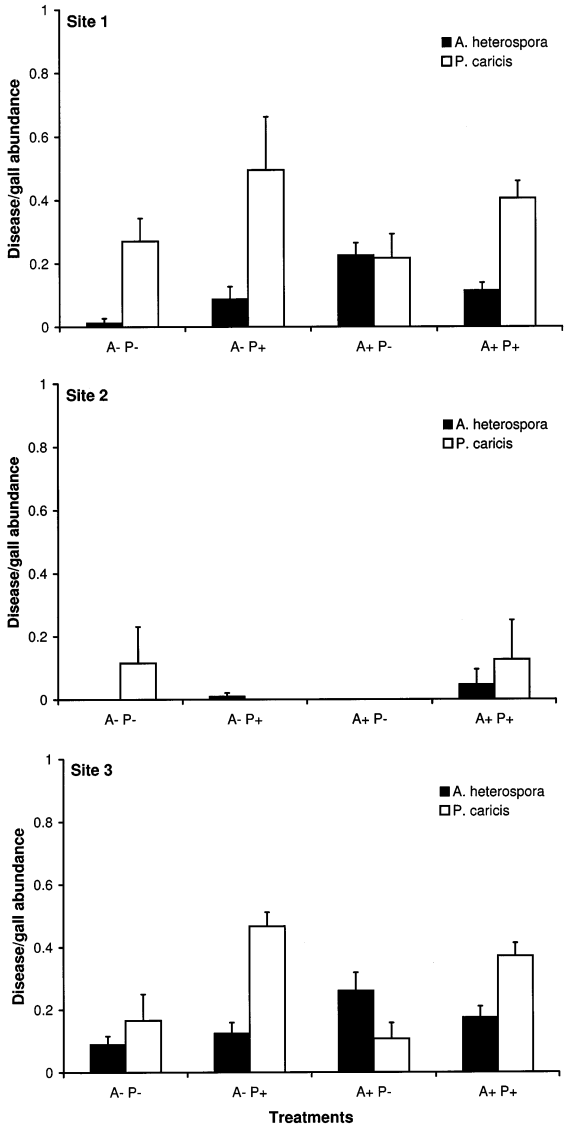

Fig. 2. Disease levels of the smut fungus *A. heterospora* and gall abundance of the gall mite *P. caricis* at the three experimental sites in 1994. Treatments are $A-/P-$: control, $A+/P-$: presence of *A. heterospora* and *P. substriatus*, $A-/P+$: presence of *P. caricis* and $A+/P+$: presence of *A. heterospora*, *P. substriatus* and *P. caricis*. Error bars denote standard error. Abundances of the two parasites were scored as the number of smutted or galled utricles divided by the number of inflorescences on the tussock.

Table 2. Results of the ANCOVA for disease severity of *A. heterospora* and gall abundance of *P. caricis* in 1994. Factors are Site, *A* – presence/absence of *A. heterospora*, *P* – presence/absence of *P. caricis*. Both *A* and *P* are nested within Site. The number of floral shoots per tussock are included in the model as a covariate (Shoots). See text for a complete description of the statistical model.

A. heterospora disease severity

Source	Site	SS	df	MS	*F*	*p*
Site		0.248	2	0.124	27.50	<0.001
Shoots		0.012	1	0.024	2.56	0.116
A(Site)	1	0.071	1	0.145	15.73	<0.001
	2	0.001	1	0.001	0.16	0.696
	3	0.081	1	0.166	18.00	<0.001
P(Site)	1	0.002	1	0.005	0.51	0.481
	2	0.002	1	0.004	0.44	0.508
	3	0.011	1	0.023	2.46	0.123
A(Site) × *P*(Site)	1	0.044	1	0.090	9.77	0.003
	2	0.001	1	0.001	0.16	0.696
	3	0.025	1	0.050	5.43	0.024
Error		0.212	47	0.005		

P. caricis gall abundance

Source	Site	SS	df	MS	*F*	*p*
Site		0.721	2	0.360	11.10	<0.001
Shoots		0.006	1	0.013	0.19	0.662
A(Site	1	0.036	1	0.73	1.10	0.301
	2	0.001	1	0.001	0.02	0.887
	3	0.026	1	0.053	0.80	0.375
P(Site)	1	0.231	1	0.471	7.11	0.010
	2	0.001	1	0.003	0.04	0.846
	3	0.363	1	0.741	11.19	0.002
A(Site) × *P*(Site)	1	0.001	1	0.002	0.02	0.879
	2	0.500	1	0.101	1.53	0.223
	3	0.002	1	0.004	0.06	0.812
Error		1.526	47	0.066		

teraction strength measures the magnitude of the effect of one species on an other, and is widely used in community ecology (Laska and Wootton 1998, McCallum 2000). There are several ways to estimate interaction strengths from field data (Laska and Wootton 1998, McCallum 2000). We used the method proposed by Wootton (1994) that estimates per capita interaction strength. This method circumvents problems associated with differences in densities or abundances between two interacting species, which are known to influence the estimates of interaction strength (Laska and Wootton 1998). The method also avoids problems associated with equilibrium assumptions, so it can be applied in a wide variety of situations (Laska and Wootton 1998). The interaction strength between two species I_{ij} is defined as the effect on focal species i when removing competitor j and it can be calculated as

$$I_{ij} = \log\left(\frac{N_{ij+}}{N_{ij-}}\right)\frac{1}{N_j} \quad (1)$$

where N_{ij+} and N_{ij-} are the abundances of the focal species when the potential competitor is present and absent, respectively, and N_j is the abundance of the competitor species when present with the focal species.

We used Eq. (1) to estimate the interaction strength of the competitive interaction between *A. heterospora* and *P. caricis*, using total number of infected utricles as estimates of the abundance of the two species. We estimated interaction strengths for both years (1994 and 1995) and for both species reciprocally.

Results

Abundances of the two parasites were generally higher in 1995 than in 1994 (Table 1). Abundances of the two parasites were scored as the number of smutted or galled utricles divided by the number of inflorescences on the tussock. The extremely low levels of both parasites at site 2 in 1994 was caused by an early-season flooding of that site.

The presence of *P. caricis* acted to reduce disease levels of *A. heterospora* when the two species were occurring together and this effect was stronger at site 1 (Fig. 2). On the other hand, *A. heterospora* had no noticeable effect on gall abundance of *P. caricis*. We found significant treatment effects of both the addition

Table 3. Results of the ANCOVA for disease levels of *A. heterospora* and gall abundance of *P. caricis* in 1995. Factors are Site, *A* – presence/absence of *A. heterospora*, *P* – presence/absence of *P. caricis*. Both *A* and *P* and their interaction are nested within Site. The number of floral shoots per tussock are included in the model as a covariate (Shoots). See text for a complete description of the statistical model.

A. heterospora disease severity

Source	Site	SS	df	MS	*F*	*p*
Site		0.131	2	0.065	13.66	<0.001
Shoots		0.019	1	0.019	3.86	0.055
A(Site)	1	0.350	1	0.350	72.97	<0.001
	2	0.461	1	0.461	96.28	<0.001
	3	0.437	1	0.437	91.33	<0.001
P(Site)	1	0.054	1	0.054	11.23	0.002
	2	0.065	1	0.065	13.55	<0.001
	3	0.182	1	0.182	38.06	<0.001
A(Site) × *P*(Site)	1	0.129	1	0.129	26.83	<0.001
	2	0.081	1	0.081	16.83	<0.001
	3	0.151	1	0.151	31.61	<0.001
Error		0.225	47	0.0048		

P. caricis gall abundance

Source	Site	SS	df	MS	*F*	*p*
Site		0.030	2	0.015	0.74	0.483
Shoot		0.023	1	0.023	1.13	0.293
A(Site)	1	0.228	1	0.228	11.08	0.002
	2	0.058	1	0.058	2.84	0.099
	3	0.043	1	0.043	2.11	0.153
P(Site)	1	0.619	1	0.619	30.07	<0.001
	2	0.422	1	0.422	20.51	<0.001
	3	0.610	1	0.610	29.67	<0.001
A(Site) × *P*(Site)	1	0.171	1	0.171	8.33	0.006
	2	0.004	1	0.004	0.18	0.670
	3	0.111	1	0.111	5.38	0.025
Error		0.967	47	0.0206		

of *P. caricis* on gall abundance and *A. heterospora* on disease levels in 1994 (Table 2). However, the interaction terms were only significant for *A. heterospora* disease levels while the interaction terms for gall abundance of *P. caricis* were low and non-significant (Table 2, Fig. 2).

In 1995 the competitive effects were consistent over the three experimental sites and interspecific competition between *A. heterospora* and *P. caricis* resulted in reduced disease levels of *A. heterospora* and lower gall abundance of *P. caricis* when the two species co-occurred on the same tussock. We again found significant effects of both treatments (Table 3). However, for this year the interaction terms were highly significant for both *A. heterospora* disease levels and abundance of *P. caricis* galls. Inspection of the means for each treatment combination shows that the presence of a competitor resulted in significant reduction in infestation levels for both *A. heterospora* and *P. caricis* (Fig. 3).

The estimates of interaction strength are given in Table 4. The interaction coefficients are all negative, indicating that presence of a competitor acts to reduce abundance of the focal species. The magnitude of the interaction strength is larger for *A. heterospora* in both of the years of the study. Using each estimated interaction coefficient as an independent data point, this difference is significant (paired *t*-test, $t = -3.39$, $df = 4$). This thus suggests that interspecific competition between *A. heterospora* and *P. caricis* is asymmetric, with *A. heterospora* suffering more from the competitive interactions than *P. caricis*.

Discussion

The results from our factorial experiment suggest that negative interactions occur between *A. heterospora* and *P. caricis*, presumably due to competition when infecting the same resource. A weak competitive effect was found for *A. heterospora* in 1994, while both species showed clear evidence of competition in 1995. It is not surprising that we found indication of interspecific competition between these two species. In their review of interspecific competition among phytophagous insects Denno et al. (1995) suggested that the probability of competition was heavily influenced by both life history and feeding styles of the involved species. Specific traits that correlated with high levels of interspecific competition included low mobility, the use of discrete feeding resources (such as fruits, cones or seeds) and a very

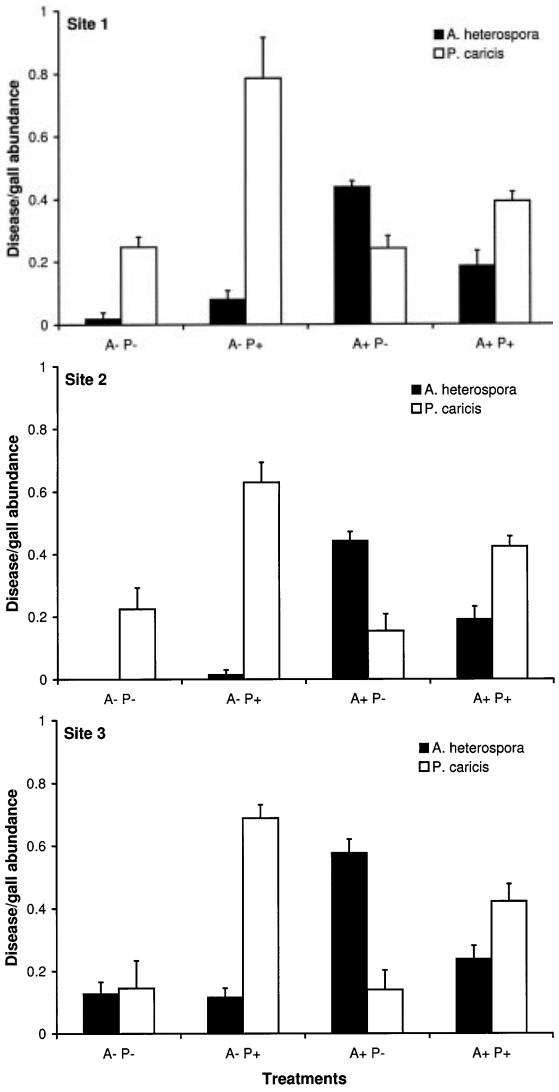

Fig. 3. Disease levels of the smut fungus *A. heterospora* and gall abundance of the gall mite *P. caricis* at the three experimental sites in 1995. Notation in the figure follows that in Fig. 2.

narrow host range. All these factors are characteristic for both *A. heterospora* and *P. caricis*. Both species depend exclusively on the developing seeds (the number of utricles on a plant) of *C. nigra* to complete the developmental cycle and have a very narrow host range (*P. caricis* is only found on *C. nigra* while *A. heterospora* are known to infect *C. nigra* and some closely related taxa). Furthermore, *P. substriatus* beetles, which are the primary vector for short distance dispersal of *A. heterospora*, have very low mobility (Ingvarsson et al. 1997). *P. caricis*, on the other hand, have high mobility but dispersal is restricted to a very short period early in the summer. However, developing larvae feed exclusively within a single utricle of the host plant, with no way to disperse until development is complete.

Data from our experiment also suggest that competition between the two species is asymmetric, with *A. heterospora* being the species suffering most from the effects of competition. Interaction strength, which measures how focal species abundance changes in the presence of a competitor, was about twice as large for *A. heterospora* (-0.034) compared to *P. caricis* (-0.019) (Table 4). Asymmetries in the effects of interspecific competition is very common; in the review by Denno et al. (1995), in over 80% of the cases in which interspecific competition occurred were the effects of competition asymmetric between the involved species. A common reason for asymmetries in the competitive effects is when early arrival to a resource results in preemption or physical exclusion from the resource of later arriving competitors. *P. caricis* generally infects the developing utricles very early in the season, at the time of anthesis, while *A. heterospora* infection usually takes place a week or so later. Thus, when *P. caricis* is present a large fraction of the developing utricles may not be available for infection by *A. heterospora*. Moreover, *A. heterospora* is, to a large extent, dependent on *P. substriatus* beetles for successful transmission and infection, at least over short distances, such as within a single host population (Ericson et al. 1993, Ingvarsson and Ericson 1998). *P. substriatus* also oviposits in developing utricles and they further require successful infection by *A. heterospora*, since developing *P. substriatus* larvae feed exclusively on the spores and hyphae of the fungus (Ingvarsson and Ericson 1998). The transmission of *A. heterospora* is therefore to a large extent determined by the oviposition behavior of the individual *P. substriatus* beetles (Ingvarsson and Ericson 1998). If *P. substriatus* beetles are actively avoiding utricles where mites have oviposited, this would lead to even more repulsed distributions of *A. heterospora* and

Table 4. Per-capita interaction strengths calculated using Eq. (1). No data were available to calculate interaction strength at site 2 in 1994. See text for further details.

	1994		1995	
Site	*A. heterospora*	*P. caricis*	*A. heterospora*	*P. caricis*
1	−0.039	−0.008	−0.041	−0.029
2	–	–	−0.039	−0.038
3	−0.025	−0.004	−0.045	−0.017
Average	−0.021	−0.006	−0.042	−0.028

P. caricis. Along similar lines it is not unreasonable to think that mites can discriminate between healthy and smut infected utricles, even in the early stages of *A. heterospora* infection. Since fungal infection will eventually lead to the destruction of the developing utricle, mite larvae developing within an infected utricle will probably not survive in a smut infected utricle.

We only found strong evidence for interspecific competition between *A. heterospora* and *P. caricis* in one year of the study (1995). In 1994 *A. heterospora* showed signs of suffering from interspecific competition but gall abundance of *P. caricis* was not negatively affected by the presence of *A. heterospora*. It is worth noting that disease levels were lower in 1994 than in 1995 and strong negative effects of interspecific competition may thus only be apparent in years when parasite levels are high. This agrees with data from a four-year survey where we found large year-to-year variations in average parasite levels of both *A. heterospora* and *P. caricis* (Ingvarsson and Ericson 1998). Interestingly, we only found repulsed distributions of *A. heterospora* and *P. caricis* on individual plants in years when both parasites occurred at high levels (Ingvarsson and Ericson 1998), once again suggesting that competitive effects between the two species may only be strong when densities of both species are high. In fact, in years when parasite levels were low, we found a positive association between the presence of the two species. It is thus possible that the two species respond in similar ways to some underlying variation in host plant quality, but that this response is muddled by interspecific competition in years favorable for parasite development (Naeem 1990, Denno et al. 1995). It is also possible that the two species are favored by the same environmental conditions, such as tussock position on the shore which may increase survival during flooding and winter storms (Ingvarsson and Ericson 1998).

While interspecific competition has recently been reinstated as an important force determining community structure for phytophagous insects (Denno et al. 1995), little attention has been directed to other plant parasites, such as fungal pathogens. A few other studies have shown that interspecific competition may also be an important process determining the occurrence and abundance of pathogenic fungi. Karban et al. (1987) showed that infection by a vascular wilt fungus induced a resistance response in infected host plants that made them more resistant to attack from spider mites. Also, Hatcher et al. (1994) showed that grazing by beetles reduced disease levels of the rust fungus *Uromyces rumicis*. Grazing by the beetle *Gastrophysa viridula* removed a large fraction of the leaf area that was potentially available for infection by *U. rumicis*. However, Hatcher et al. (1994) also showed that fungal infection was reduced in ungrazed portion of damaged leaves and even in undamaged leaves in grazed plants. Also, Shivas and Scott (1993) showed clear evidence for negative interactions between the stem blight pathogen *Phomposis emicis* and the weevil *Perapion antiquum* infecting the weed *Emex australis*. Experiments by Shivas and Scott (1993) showed that damage by the weevil induced a host response that slowed the development of the fungus. A study by Padgett et al. (1994) showed that defoliation of soybean by two phytophagous insects reduced severity and incidence of both stem canker and red crown rot.

The focus of this paper has been on whether interspecific competition may influence the occurrence of the two parasites *A. heterospora* and *P. caricis* and we have not addressed any questions relating to whether the presence of the parasites affects host plant reproduction and survival. However, recent studies have argued for taking interspecific interactions into account when studying the interplay between plants and herbivores or pathogens. Several studies have shown that the effects of multiple herbivores can induce non-additive effects on that host plant, so that the response to herbivory cannot be predicted for studies of pairwise interactions between a plant and its suite of herbivores (e.g. Strauss 1991, Hougen-Eitzman and Rausher 1994, Iwao and Rausher 1997). Thus, studies in natural populations must focus on the entire community of herbivores and pathogens to better understand what shapes plant-herbivore and plant-pathogen co-evolution.

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