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Modification of competition between two grass species by a hemiparasitic plant and simulated grazing

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Summary

Plant parasitism and herbivory are common phenomena in natural grasslands, where they may significantly affect competition between plant species. However, only few studies have simultaneously examined these two processes. We investigated whether the root hemiparasite *Odontites litoralis* ssp. *litoralis* affects the outcome of competition between two clonal graminoids, the endangered *Puccinellia phryganodes* and the common species *Agrostis stolonifera,* and whether simulated grazing affects the interaction among these three species. This study system simulates the community of early successional stages of the Bothnian Bay salt marsh meadows, which are intensively grazed by greylag geese (*Anser anser*). We conducted a factorial greenhouse experiment to study the effects of interspecific competition (one or two host species present), hemiparasitic infection (hemiparasite present or not), and simulated grazing (host clipped or not) on *Puccinellia* and *Agrostis. Puccinellia* was clearly an inferior competitor to *Agrostis*, whereas the two species did not differ as hosts for the hemiparasite. Infection by the hemiparasite reduced the aboveground biomass of *Puccinellia* and *Agrostis* by 59% and 45%, respectively. Competition with *Agrostis* decreased the biomass of parasitised *Puccinellia* by 36% and that of non-parasitised *Puccinellia* by 56%. Parasitism thus seemed to benefit *Puccinellia* indirectly by decreasing the relative competitive advantage of *Agrostis*. Moreover, parasitism increased the relative contribution of *Puccinellia* to the total aboveground host plant biomass. Simulated grazing decreased the aboveground biomass of *Agrostis* significantly more than that of *Puccinellia* and thus increased the competitive ability of *Puccinellia*. Simulated grazing of the two host species did not affect the performance of *Odontites*. These results suggest that both hemiparasitic plants and herbivory may play a significant role in the maintenance of plant species diversity by promoting competitively inferior species.

Zusammenfassung

Parasitierung und Herbivorie sind verbreitete Phänomene in natürlichen Grasländern, wo sie die Konkurrenz zwischen Pflanzenarten maßgeblich beeinflussen können. Indessen haben nur wenige Studien die beiden Prozesse gleichzeitig betrachtet. Wir untersuchten, ob der Wurzelhemiparasit *Odontites litoralis* ssp. *litoralis* das Ergebnis der Konkurrenz zwischen zwei klonalen Gräsern, der gefährdeten Art *Puccinellia phryganodes* und der häufigen Art

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Agrostis stolonifera, beeinflusst und ob sich simulierte Beweidung auf die Interaktionen zwischen den drei Arten auswirkt. Das untersuchte System bildet die Gemeinschaft der frühen Sukzessionsstadien der Salzwiesen im nördlichen Teil des Bottnischen Meerbusens nach, die intensiv von Graugänsen (*Anser anser*) beweidet werden. In einem faktoriellen Gewächshausexperiment untersuchten wir die Effekte von interspezifischer Konkurrenz (eine oder beide Wirtsarten vorhanden), des Befalls mit dem Hemiparasiten (Hemiparasit vorhanden oder nicht), und von simulierter Beweidung (Wirtspflanzen beschnitten oder nicht) auf die beiden Gräser. *Puccinellia* war *Agrostis* als Konkurrent eindeutig unterlegen, während beide Arten sich als Wirte für den Hemiparasiten nicht unterschieden. Befall durch den Hemiparasiten reduzierte die oberirdische Biomasse von *Puccinellia* und *Agrostis* um 59 bzw. 45%. Konkurrenz mit *Agrostis* verminderte die Biomasse parasitierter *Puccinellia* um 36% und die von nicht parasitierter *Puccinellia* um 56%. Parasitierung schien deshalb *Puccinellia* indirekt zu begünstigen, indem der relative Konkurrenzvorteil von *Agrostis* reduziert wurde. Außerdem erhöhte die Parasitierung den relativen Beitrag von *Puccinellia* zur oberirdischen Gesamt-Pflanzenbiomasse. Simulierte Beweidung verringerte die oberirdische Biomasse von *Agrostis* signifikant stärker als die von *Puccinellia* und stärkte somit die Konkurrenzkraft der zweiten Art. Die simulierte Beweidung der Wirtsarten beeinflusste die Performanz von *Odontites* nicht. Diese Ergebnisse legen nahe, daß sowohl hemiparasitische Pflanzen als auch Beweidung eine wichtige Rolle bei der Erhaltung der Artenvielfalt der Pflanzen spielen können, indem unterlegene Konkurrenten gefördert werden.

Keywords: *Odontites litoralis* ssp. litoralis; Clonal graminoid hosts; Hemiparasitism; Endangered plant species; Salt marsh vegetation

Introduction

Parasitic plants may significantly affect species diversity and community dynamics in grasslands (for a review see Press & Phoenix, 2005). Species diversity has been observed to increase when parasitic plants suppress competitively superior host species (e.g. Callaway & Pennings, 1998; Davies, Graves, Elias, & Williams, 1997; Pennings & Callaway, 1996), or to decrease when the competitively inferior species are suppressed (Gibson & Watkinson, 1992). In addition to parasitic plants, host plants are subjected to multiple natural enemies, for example, a variety of herbivores and pathogens. However, only few studies have simultaneously examined the effects of plant parasitism and herbivory on host performance (Goméz, 1994; Puustinen & Mutikainen, 2001; Puustinen & Salonen, 1999).

Parasitic plants and herbivores have many parallel effects on their hosts: both may display host preferences, reduce host biomass, alter host allocation patterns, modify plant community structure and dynamics, and mediate interactions between host plants and other organisms (e.g. Pennings & Callaway, 2002). Due to parasite-induced changes in host physiology and resource allocation parasitic plants may damage their hosts more than herbivores in proportion to their size (Pennings & Callaway, 2002). Because of their sedentary nature, the sphere of action of an individual parasitic plant is relatively small compared to that of many herbivores. However, given the high densities of parasitic plants observed in the field (e.g. Davies et al., 1997; Marvier, 1998; Pennings & Callaway, 1996; Snogerup, 1983), their collective impact might be substantial. The combined effects of parasitic plants and herbivores involve a complex network of both direct and indirect interactions in which the consumers may change the quality and availability of the host plants as a resource for each other (Price et al., 1986; Smith, 2000). For example, shoot herbivory is likely to decrease resource allocation to roots (e.g. Crawley, 1997), and may thus affect root parasitic plants negatively (Puustinen & Salonen, 1999). On the other hand, parasites may induce changes in host carbohydrate and nutrient concentrations and resource allocation, which are likely to affect the ability of the host plant to compensate for herbivore damage (e.g. Matthies, 1995a, b; Nowak & Caldwell, 1984; Stowe, Marquis, Hochwender, & Simms, 2000).

Using a factorial greenhouse experiment, we examined whether the root hemiparasite *Odontites litoralis* ssp. *litoralis* affects the outcome of competition between two grass species, *Puccinellia phryganodes* and *Agrostis stolonifera*. We also studied the effect of simulated grazing on the interactions among these three plant species, which commonly occur together in the Bothnian Bay salt marsh community. The salt marsh community represents the early successional stages of the shore vegetation that are characterised by a combination of intensive herbivory and a high density of hemiparasitic plants. The small perennial graminoid *P. phryganodes* is an endangered species of the low-growing salt marsh meadows in the Bothnian Bay (Ryttäri, Rautiainen, Kemppainen & Alanen, 2001). *A. stolonifera*, a common grass in these meadows, is assumed to be a superior competitor to *Puccinellia*. The meadow with the largest subpopulation of *Puccinellia* is intensively grazed by greylag geese (*Anser anser*). Only few species are not foraged, including the annual root hemiparasite *O. litoralis* ssp. *litoralis*. Thus, it is likely that the grazing delays succession and enables the persistence of *Puccinellia*. We addressed the following specific questions: (1) Do infection by a parasitic plant and simulated grazing of the host plants modify the competitive interactions between the two host plants, *Agrostis* and *Puccinellia*? If the parasitic plant or grazing have more negative effects on the presumably superior competitor *Agrostis*, they might promote the persistence of the competitively inferior *Puccinellia* by delaying succession and thus they may contribute to the maintenance of a higher species diversity of the salt marsh community. (2) Is the performance of the parasitic plant affected by simulated grazing of the host? Because the parasitic plant and the grazing herbivore may compete for host resources, we predict that the simulated grazing of the host plants has negative effects on parasite performance.

Materials and methods

Study species

The perennial graminoid *P. phryganodes* (Trin.) Scribner & Merr. (referred to as *Puccinellia* hereafter) reproduces clonally by producing easily detaching axillary shoots on the vegetative ramets. In the field, a *Puccinellia* stand is approximately 5 cm in height and the length of the stolons varies from 10 to 20 cm (Siira & Merilä, 1997). The plant produces flowers but no seed production has been reported (Sørensen, 1953). *Puccinellia* is distributed circumpolarly around the Arctic Ocean with a disjunct occurrence in the Bothnian Bay (Hultén, 1962; Siira & Merilä, 1985). *Puccinellia* is one of the first plant species colonising the newly emerged surface on the land uplift areas and on tidal flats in arctic salt marshes (Jefferies, Jensen & Abraham, 1979). The coast of the Bothnian Bay is flat and strongly affected by post-glacial land uplift (ca. 7 mm per year; Vermeer & Kakkuri, 1988), which leads to a distinct succession of plant communities on the seashore (Vartiainen, 1980). Because cattle grazing and hay making have almost totally ceased, large-scale overgrowth by taller vegetation has taken place in the meadows (e.g. Jutila, 1999). Simultaneously, *Puccinellia* populations have greatly decreased in size; currently only five populations remain in the Baltic Sea area. The plant material for the experiment was collected from the largest population that is located on the Isomatala salt marsh meadow. This meadow is located on a 1 km^2 islet on the southern part of the island of Hailuoto, Finland (24°46′N, 64°56′E). The Isomatala meadow is intensively grazed by breeding and moulting greylag geese (Niemelä & Markkola, 2004; Siira & Merilä, 1997).

A. stolonifera L. (referred to as *Agrostis* hereafter) is a common perennial grass occurring in Europe, Asia and North America (Hultén, 1962). It is abundant on the shores of the Bothnian Bay, and is often the dominant species in the meadow zone just above the mean water line (Widén, 1971). It reproduces both vegetatively and sexually (Widén, 1971). The height of *Agrostis* varies from 15 to 100 cm and the stolons may be up to 2 m long (Widén, 1971).

The annual root hemiparasite *O. litoralis* (Fr.) Fr. subsp. *litoralis* (referred to as *Odontites* hereafter) is often abundant in the salt marshes (Snogerup, 1983). *Odontites* can survive without a host plant and is thus partially autotrophic. It is assumed to be a weak competitor (Snogerup, 1983). The seedlings of *Odontites* are sensitive to being submerged. During the southern winds the seedlings occasionally become submerged when the level of sea water rises and the salt marsh meadows in the Bothnian Bay become flooded. If submergence lasts more than several days, as happens in certain years, almost all seedlings are destroyed (M. Niemelä, personal observation).

Experimental design

Stolons consisting of more than five axillary shoots were collected from 15 individuals of both *Puccinellia* and *Agrostis* occurring in the meadow of Isomatala in October 2001. The distance between the collected stolons varied between 1 and 5 m. At the same time, seeds of 100 randomly selected *Odontites* individuals were collected from the same meadow. A pooled seed sample was sown into a mixture of mull and sand, and stratified at +5 °C in the dark during November–March. The seeds of *Odontites* started to germinate in the middle of March. Individual shoots of *Puccinellia* and *Agrostis* were planted into a mixture of peat and sand (1:2) and grown in a greenhouse (+6 °C and 18 h light) from November 2001 to March 2002. During this time, the individual shoots formed multiple shoots with roots. In late March 2002, rooted individual shoots of both grass species were assigned randomly to the treatments (see below). At this time, the shoots of both species had 2–5 leaves and the heights of the shoots were 5 and 10 cm for *Puccinellia* and *Agrostis*, respectively. In early April, four *Odontites* seedlings (ca. 2 cm tall, with 2–4 leaves) were planted with *Puccinellia* and/or *Agrostis* or without a host plant into 1 L pots filled with a mixture of mull, fertilised and limed peat, sand and Leca pellets (inorganic porous growing medium) (4:4:1:1 in volumes). A slowly-releasing fertiliser Nutricote T 180 (CHISSO-ASAHI, Japan) 3 g L^{-1} (N–P–K:14–6–12% DW) was also added to the mixture. *Odontites* seedlings were planted at approximately 2 cm distance from the host plant. In the treatments with two host plants, the seedlings were planted between the host plants. One week later the number of *Odontites* was reduced to one per pot.

The experiment was conducted according to a factorial design with the following factors: host species (*Puccinellia*, *Agrostis*), interspecific competition (one or two host species present), hemiparasitic infection (hemiparasite present or not) and simulated grazing (hosts clipped or not). Only one individual of each species was present in each replicate of these treatments, i.e. intraspecific competition was not included whereas the occurrence of interspecific competition varied. In addition, we grew the hemiparasitic *Odontites* alone. There were 15 replicates in each treatment combination. The pots were arrranged to a randomised block design in the greenhouse. The plants were grown for about 3 months (April–June) at 18–20/15–18 °C day/night temperature and watered regularly. They received artificial light 18 h d^{-1} provided with SON-T Agro 400 W/HPI-T Plus 400 W lamps (Philips AB). Light intensity was 22 W m^{-2} and PAR 120 Em^{-2} s^{-1} $\times 10^{-6}$. In addition, plants received natural light. During the experiment, day length increased from 13.5 to 22 h per day from April to June, respectively. The simulated grazing treatment (clipping) was conducted once, 6 weeks after planting, when *Odontites* started to flower and the grass shoots were on the average 13 cm and 42 cm in height for *Puccinellia* and *Agrostis*, respectively. The shoots of both grass species were clipped with scissors to the height of 2–3 cm, leaving *Odontites* intact. Clipping reduced shoot length on average by 93% in *Agrostis* and 75% in *Puccinellia*. Clipping roughly simulates grazing by geese for two reasons. First, during the moulting period from early June to mid July, the geese graze the meadow at the lowest to a height of 2–3 cm while *Odontites* is left intact (*M. Niemelä*, personal observation). Secondly, after the moulting period grazing pressure decreases considerably as the geese disperse to other feeding grounds. Consequently, the vegetation recovers from mid-July till the end of the growing season. Simulating this, the plants were allowed to regrow for one and a half months until the end of the experiment.

The plants were harvested 3 months after planting, when *Odontites* capsules had fully ripened. Roots were carefully separated from the soil and washed on a sieve. Twenty root pieces (each 3–4 cm in length) of each host plant grown with the hemiparasite were collected from all host combinations and stored in 50% ethanol. The number of haustoria of *Odontites* per unit length of host roots was counted under a preparation microscope. For pots with the two host plants growing together, the roots could not be separated for biomass analyses with sufficient accuracy. The shoots and the rest of the roots of all three species were weighed after drying them for 48 h at 50 °C. For *Odontites* shoot height was measured and the number of branches and capsules was counted.

Data analysis

Host performance was examined separately for *Puccinellia* and *Agrostis* using ANOVA with competition, parasitism, and simulated grazing as fixed factors, and block as a random factor. Using cases in which both host species were present, the effects of parasitism and grazing on the relative contribution of *Puccinellia* to the total aboveground host biomass were examined using ANOVA. Only the treatments in which the host plants had grown alone or with *Odontites* were included in the analysis of host root biomass.

Hemiparasite performance was examined using two data sets. First, to study the importance of host plant presence we used data of *Odontites* grown alone and *Odontites* grown with the unclipped hosts. Second, to study the effects of host competition and host grazing on *Odontites* performance we used data of *Odontites* grown in the three host treatments (*Puccinellia* or *Agrostis* or both) in both control and simulated grazing treatments. The frequency of hemiparasite haustoria on host roots was compared using ANOVA, including only the cases in which a single host plant was present. Effects of competition and simulated grazing on frequency of haustoria was analysed using ANOVA separately for both host species. To meet the assumptions of parametric ANOVA, logarithmic transformations were conducted for the number of *Odontites* capsules, host aboveground and root biomass.

Results

Host performance

Competition, simulated grazing, and parasitism reduced the aboveground biomass of both host species (Table 1). However, competition and parasitism caused a relatively greater biomass reduction in *Puccinellia* (Fig. 1A). When averaged over all other treatments, competition decreased the final aboveground biomass of *Puccinellia* by 52% and that of *Agrostis* by 29% compared to the cases without competition, suggesting that *Puccinellia* was the inferior competitor. Similarly, parasitism reduced the biomass of *Puccinellia* and *Agrostis* by 59% and 45%, respectively. In contrast, simulated grazing decreased relatively more the aboveground biomass of *Agrostis* (by 73%) than that of *Puccinellia* (by 53%) when compared to the unclipped treatments.

A significant interaction between competition and parasitism was found for the biomass of *Puccinellia* (Table 1), indicating that the effect of competition

Table 1. Results of three-way ANOVA testing for the effects of competition, simulated grazing (clipping) and parasitism on the aboveground biomass of host species

	Puccinellia phryganodes			*Agrostis stolonifera*		
	df	*F*	*P*	df	*F*	*P*
Competition	1	38.866	<0.001	1	10.613	0.002
Clipping	1	54.155	<0.001	1	230.644	<0.001
Parasitism	1	79.158	<0.001	1	76.770	<0.001
Competition × clipping	1	0.004	0.951	1	0.084	0.772
Competition × parasitism	1	5.518	0.021	1	0.281	0.598
Clipping × parasitism × clipping	1	0.050	0.823	1	2.093	0.152
Competition × parasitism	1	0.071	0.791	1	0.370	0.545
Block	13	3.646	<0.001	14	7.584	<0.001
Error	77			79		

Error mean square was 0.038 for *Puccinellia phryganodes* and 0.036 for *Agrostis stolonifera*.

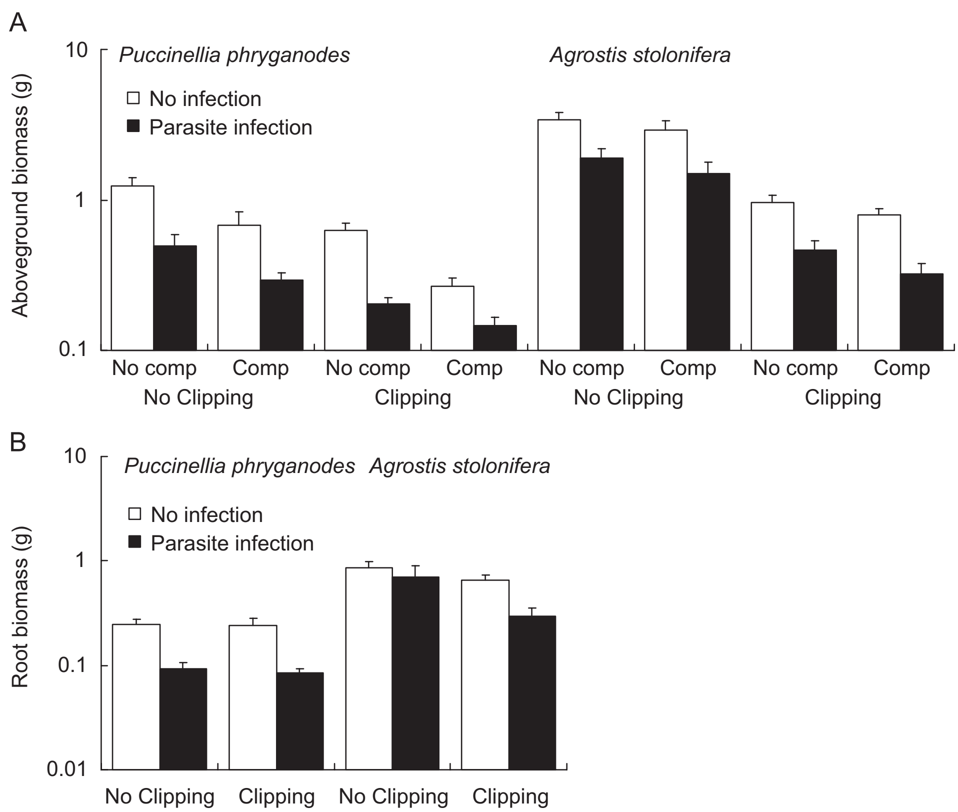

Fig. 1. Aboveground biomass (mean + 1 SE; A) of *Puccinellia phryganodes* and *Agrostis stolonifera* in the different treatments of clipping, competition (Comp), and parasitism. (B) Root biomass (mean + 1 SE) of *Puccinellia phryganodes* and *Agrostis stolonifera* grown with (parasite infection) or without (no infection) the hemiparasite, *Odontites litoralis*.

depended on the presence of the hemiparasite. In non-parasitised *Puccinellia* competition with *Agrostis* reduced the biomass by 56%, whereas in parasitised plants reduction was only 36% when averaged over the clipped and non-clipped plants (Fig. 1A). This suggests that parasitism decreased the competitive pressure of *Agrostis* against *Puccinellia*.

While the total aboveground host biomass per pot was reduced, the relative proportion of *Puccinellia* was increased by both simulated grazing ($F_{1,27} = 27.77$, $P < 0.001$) and parasitism ($F_{1,27} = 4.79$, $P = 0.037$; Fig. 2). This further suggests that *Puccinellia* may indirectly benefit from both grazing and parasitism due to reduced competition. There was no statistically significant interaction between simulated grazing and parasitism ($F_{1,27} = 2.38$, $P = 0.135$).

The root biomass of *Agrostis* was significantly higher than that of *Puccinellia* (three-way ANOVA:

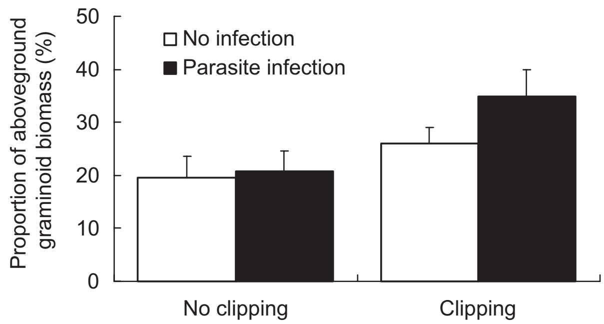

Fig. 2. Relative contribution of *Puccinellia phryganodes* to the total aboveground graminoid biomass (mean + 1 SE) in control and simulated grazing (clipping) treatments and in relation to the hemiparasite infection.

$F_{1,80} = 282.46$, $P<0.001$; Fig. 1B). Both parasitism (three-way ANOVA: $F_{1,80} = 87.26$, $P<0.001$) and simulated grazing (three-way ANOVA: $F_{1,80} = 10.98$, $P = 0.001$) decreased the root biomass. In *Puccinellia* parasitism reduced root biomass by 64% and in *Agrostis* by 36% (Fig. 1B). There was a significant interaction between species and simulated grazing (three-way ANOVA: $F_{1,80} = 9.65$, $P = 0.003$) indicating that the two species responded differently to grazing. Indeed, simulated grazing decreased the root biomass of *Agrostis* by 40% but did not affect the root biomass of *Puccinellia* (Fig. 1B).

Parasite performance on different host species

Performance of the hemiparasitic *Odontites* was affected by the presence of the host (one-way ANOVA: $F_{3,34} = 15.45$, $P<0.001$): the number of capsules was significantly lower when the hemiparasite was grown without a host than when grown with either of the host species (*Puccinellia* or *Agrostis*) or with both of them (Fig. 3). Host species and simulated grazing did not significantly affect the number of capsules (two-way ANOVA: $F_{2,57} = 2.60$, $P = 0.083$ and $F_{0.004} = 2.60$, $P = 0.950$, respectively). The impacts of the presence of the host and host species on shoot height and biomass of *Odontites* were qualitatively similar to those on capsule production (data not shown).

When the hosts were grown without interspecific competition, the frequency of *Odontites* haustoria on host roots (number of haustoria cm^{-1}) was higher in *Puccinellia* than in *Agrostis* (0.54 ± 0.05, mean $\pm$ 1SE, and 0.20 ± 0.03, respectively; two-way ANOVA: $F_{1,35} = 31.31$, $P<0.001$). When *Agrostis* was present as an additional host, the frequency of *Odontites* haustoria on *Puccinellia* roots decreased to 0.31 ± 0.04, i.e. by 42% (two-way ANOVA: $F_{1,32} = 9.52$, $P = 0.004$; Fig. 4). The presence of *Puccinellia* did not result in a significant reduction of haustoria number on *Agrostis* roots

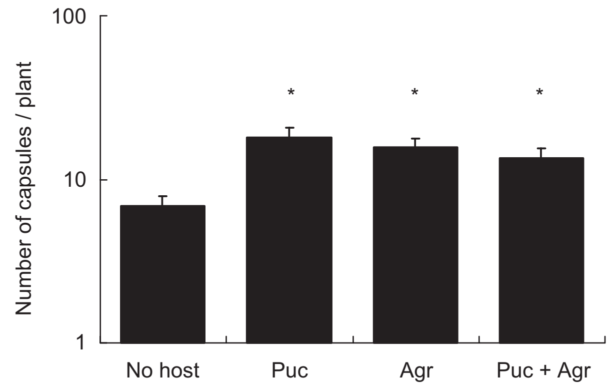

Fig. 3. Number of capsules (mean + 1 SE) of *Odontites litoralis* grown without hosts (no host) or with the two host species (Puc = *Puccinellia phryganodes*, Agr = *Agrostis stolonifera*). Asterisks indicate significant differences ($P<0.001$) between the no-host treatment and each host treatment (Dunnett's *t*-tests).

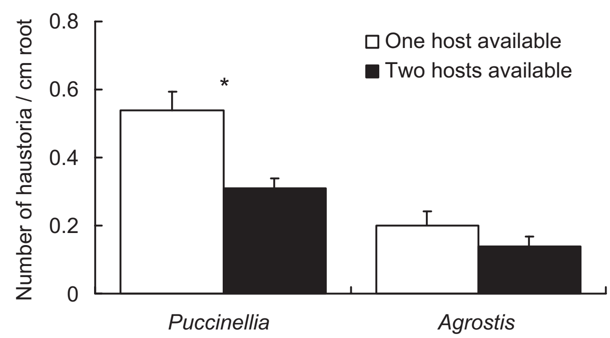

Fig. 4. Number of haustoria (mean + 1 SE) of *Odontites litoralis* on the roots of *Puccinellia phryganodes* and *Agrostis stolonifera* when either one (*Puccinellia* or *Agrostis*; white bars) or two (both *Puccinellia* and *Agrostis*; black bars) host species were present. Data from clipped and non-clipped host plants are pooled. The asterisk indicates a significant difference ($P<0.01$) between the two competition treatments.

(0.14 ± 0.03, i.e. a decrease by 29%; two-way ANOVA: $F_{1,34} = 3.38$, $P = 0.075$; Fig. 4). Simulated grazing of the host had no effect on the amount of haustoria on host roots (two-way ANOVA: $F_{1,32} = 2.15$, $P = 0.152$ and $F_{1,34} = 0.001$, $P = 0.972$ for *Puccinellia* and *Agrostis*, respectively). No interactions were observed between competition and simulated grazing for the number of haustoria (two-way ANOVA: $F_{1,32}<0.001$, $P = 0.985$ and $F_{1,34} = 2.33$, $P = 0.137$ for *Puccinellia* and *Agrostis*, respectively).

Discussion

Effects of hemiparasite and simulated grazing on host performance

Our results show that *Puccinellia* was an inferior competitor to *Agrostis* because interspecific competition was more detrimental to *Puccinellia* than to *Agrostis*. Secondly, our results suggest that in spite of the more negative direct effects of the hemiparasite infection on *Puccinellia* than on *Agrostis*, parasitism decreased the relative competitive advantage of the superior competitor. Moreover, parasitism increased the relative contribution of *Puccinellia* to the total aboveground host biomass. Our results are in accordance with the findings of previous experimental studies in which hemiparasitic plants have been found to affect the outcome of competition between their host species (Gibson & Watkinson, 1991; Matthies, 1996). Previously, hemiparasitic plants have been found to have more detrimental impacts either on competitively superior or inferior host species. For example, *Rhinanthus serotinus* suppressed more and performed better on a competitively stronger host species (*Trifolium repens*) and thus benefited the weaker competitor (Gibson & Watkinson, 1991). In contrast, *Melampyrum arvense* suppressed most and had a higher performance on the weakest competitor (*Medicago sativa*; Matthies, 1996). In our study *Odontites* suppressed relatively more the weaker competitor *Puccinellia*. However, when hosts were clipped, the infection by *Odontites* seemed to benefit *Puccinellia*. This was apparently due to the more detrimental effects of clipping on parasitised *Agrostis* than on parasitised *Puccinellia*.

If the amount of hemiparasite haustoria attached to host roots reflects the host preference of the parasitic plant, as has been shown by Gibson and Watkinson (1989), our results suggest that *Puccinellia* was preferred by *Odontites*. However, hemiparasite performance was not higher on *Puccinellia*. In previous studies the number of haustoria has been found to correlate positively with hemiparasite performance and with the damage experienced by the host (Gibson & Watkinson, 1991; Keith, Cameron, & Seel, 2004). In our study, a positive correlation was found only between the number of haustoria and the host damage, i.e. both the number of haustoria and the damage induced by the hemiparasite were higher in *Puccinellia*. Thus, selective parasitism and/or depression of the competitively superior *Agrostis* do not explain the modification of competition by the hemiparasite observed here as they do in the study of Gibson and Watkinson (1991). The presence of *Agrostis* reduced the haustoria density on roots of *Puccinellia*, which might provide a more plausible explanation for the hemiparasite-induced increase in the competitive ability of *Puccinellia*. According to this explanation, simultaneous presence of *Agrostis* may have provided *Puccinellia* a partial escape from the hemiparasite by offering an alternative host resource.

In combination, parasitism and simulated grazing decreased aboveground biomass of both species by more than 80%. However, simulated grazing decreased the biomass of *Agrostis* significantly more than that of *Puccinellia* partially because the two species were different in size when clipped and thus the relative amount of removed biomass differed between the species. Furthermore, compared to grazing, the effect of competition on *Agrostis* was minor. Thus, these results suggest that the relative benefit gained by *Puccinellia* in terms of competitive ability due to grazing was mainly caused by the highly negative effect of the simulated grazing on the competing *Agrostis*. Our results are in accordance with, for example, those of Belsky (1992) that showed that grazing by large mammals in the grasslands of East Africa suppressed taller graminoids to the benefit of small graminoid species.

Parasite performance

Contrary to our expectations, simulated grazing of the two host species did not affect the performance of the hemiparasite. Perennial graminoids have large root systems with stored resources, which could enable survival and reproduction of the hemiparasite even when the host's aboveground parts are removed. Differences in root reserves may also explain the results of a previous study, in which the defoliation of a perennial host, *Poa pratensis*, had no effect on the hemiparasitic *R. serotinus*, whereas defoliation of an annual host, *Poa annua,* decreased the total biomass and number of flowers of the hemiparasite (Puustinen & Salonen, 1999). In another study, the hemiparasites *Odontites rubra* and *R. serotinus* survived the removal of the shoots of their host plant, *M. sativa* (Matthies, 1995a). This was suggested to be enabled by either the extraction of resources from the host roots or by sufficient functioning of the hemiparasite's own root system (Matthies, 1995a). Further, as host shoots and roots generally compete for resources, removal of the main part of the host shoots may leave larger proportion of host root resources available for the hemiparasite. This kind of allocation shift in grazed plants has been reported to occur commonly in short-term herbivory experiments (Bardgett, Wardle, Yeates, 1998).

Herbivory of the hosts may also have slight positive effects on the autotrophic performance of the hemiparasitic plant. Removal of host shoots by simulated grazing partially released *Odontites* from light competition with the host, which may have enhanced autotrophic carbon acquisition of the hemiparasite. This may partly explain the lack of negative effects of host clipping on hemiparasite performance. Similarly, repeated cutting of the surrounding vegetation has been suggested to reduce competition with host plants in the hemiparasitic *Euphrasia stricta* (Hellström, Rautio, Huhta, & Tuomi, 2004). For example *R. serotinus* and *O. rubra* (Matthies, 1995a) as well as *Rhinanthus minor*

(Keith et al., 2004) have been shown to suffer from aboveground competition with their hosts. In the present experiment, the relatively late clipping date in relation to the phenology of the hemiparasite may also partly explain the non-significant effect of host clipping on hemiparasite performance.

Both graminoids, *Puccinellia* and *Agrostis,* proved to be equally suitable hosts for the hemiparasitic *Odontites*. In a previous study, the performance of *O. litoralis* ssp. *litoralis* varied depending on the host identity even though the hemiparasite was able to survive with several host species. Performance of the hemiparasite varied significantly even within one host genus: with *Festuca rubra* as the host, none of the hemiparasite seedlings survived to a seed-producing adult, whereas with *F. arundinacea* all seedlings survived (Snogerup, 1982). Differences in the effects of host species on hemiparasite performance have also been obtained for other *Odontites* species (Snogerup, 1982; Matthies, 1998).

Implications to species diversity of the salt marsh community

Limitations originating from experimental conditions restrict the extrapolation of our results to the plant community level. Our experimental conditions differ from the conditions in the field in terms of the simulated grazing treatment (discussed in methods), short duration of the experiment, lack of density effect and lack of intraspecific competition in our experiment. However, our results have certain implications for interpreting the effects of parasitism and herbivory on the competitive interactions and species diversity. First, in the field the hemiparasitic *Odontites* is not foraged by geese whereas the neighbouring species are largely grazed, which increases availability of light for the hemiparasite. This together with the fact that *Odontites* was able to reproduce successfully in spite of the removal of the main part of the host shoots at least partly explains how geese grazing may enable *Odontites* to prevail in the salt marsh plant community. Secondly, our results suggest that although *Agrostis* maintained its dominance in terms of final aboveground biomass, simulated grazing improved the relative competitive status of *Puccinellia*, the inferior competitor. Thus, grazing by geese may be an important factor in slowing down the replacement of *Puccinellia* by *Agrostis* and other stronger competitors of the salt marsh community. In addition, our results suggest that the hemiparasitic *Odontites* may indirectly contribute to the maintenance of *Puccinellia* via suppressing its competitor *Agrostis*. However, the wide yearly variation in the abundance of the hemiparasite (M. Niemelä, personal observation) may reduce the influence of the hemiparasite on the host plants. Such yearly variation also emphasises the importance of the more regular impact of goose grazing. However, in addition to the biotic factors studied here, in the long term and at a larger spatial scale, the persistence of *Puccinellia* in the salt marsh depends on its ability to disperse to the continuously emerging new competition-free habitats created by land uplift.

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References

Bardgett, R. D., Wardle, D. A., & Yeates, G. W. (1998). Linking above-ground and below-ground interactions: How plant responses to foliar herbivory influence soil organisms. *Soil Biology and Biochemistry*, *30*, 1867–1878.

Belsky, A. J. (1992). Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science*, *3*, 187–200.

Callaway, R. M., & Pennings, S. C. (1998). Impact of parasitic plant on the zonation of two salt marsh perennials. *Oecologia*, *114*, 100–105.

Crawley, M. J. (1997). Plant–herbivore dynamics. In M. J. Crawley (Ed.), *Plant ecology* (pp. 401–474). Oxford: Blackwell Science.

Davies, D. M., Graves, J. D., Elias, C. O., & Williams, P. J. (1997). The impact of *Rhinanthus* spp. on sward productivity and composition: Implications for the restoration of species-rich grasslands. *Biological Conservation*, *82*, 87–93.

Gibson, C. C., & Watkinson, A. R. (1989). The host range and selectivity of a parasitic plant: *Rhinanthus minor*. *Oecologia*, *78*, 401–406.

Gibson, C. C., & Watkinson, A. R. (1991). Host selectivity and mediation of competition by the root hemiparasite *Rhinanthus minor*. *Oecologia*, *86*, 81–87.

Gibson, C. C., & Watkinson, A. R. (1992). The role of the hemiparasitic annual *Rhinanthus minor* in determining grassland community structure. *Oecologia*, *89*, 62–68.

Goméz, J. M. (1994). Importance of direct and indirect effects in the interaction between a parasitic angiosperm (*Cuscuta epithymium*) and its host plant (*Hormatophylla spinosa*). *Oikos*, *71*, 97–106.

Hellström, K., Rautio, P., Huhta, A.-P., & Tuomi, J. (2004). Tolerance of an annual hemiparasite, *Euphrasia stricta* agg., to simulated grazing in relation to the host environment. *Flora*, *199*, 247–255.

Hultén, E. (1962). The circumpolar plants I. Vascular cryptogams, conifers, monocotyledons. *Kungliga Svenska Vetenskapsakademiska Handlingar (4. ser.)*, *8*, 1–340.

Jefferies, R. L., Jensen, A., & Abraham, K. F. (1979). Vegetational development and the effect of geese on vegetation at La Pérouse Bay, Manitoba. *Canadian Journal of Botany*, *57*, 1439–1450.

Jutila, H. (1999). Effect of grazing on vegetation of shore meadows along the Bothnian Sea, Finland. *Plant Ecology*, *140*, 77–88.

Keith, A. M., Cameron, D. D., & Seel, W. E. (2004). Spatial interactions between the hemiparasitic angiosperm *Rhinanthus minor* and its host are species-specific. *Functional Ecology*, *18*, 435–442.

Marvier, M. A. (1998). Parasite impacts of host communities: Plant parasitism in a California coastal prairie. *Ecology*, *79*, 2616–2623.

Matthies, D. (1995a). Parasitic and competitive interactions between the hemiparasites *Rhinanthus serotinus* and *Odontites rubra* and their host *Medicago sativa*. *Journal of Ecology*, *83*, 245–251.

Matthies, D. (1995b). Host–parasitic relations in the root hemiparasite *Melampyrum arvense*. *Flora-Jena*, *190*, 383–394.

Matthies, D. (1996). Interactions between the root hemiparasite *Melampyrum arvense* and mixtures of host plants: Heterotrophic benefit and parasite-mediated competition. *Oikos*, *75*, 118–124.

Matthies, D. (1998). Influence of the host on growth and biomass allocation in the two facultative root hemiparasites *Odontites vulgaris* and *Euphrasia minima*. *Flora-Jena*, *193*, 187–193.

Niemelä, M., & Markkola, J. (2004). Merihanhi maiseman ja kasvillisuuden muokkaajana. In P. Nummi, & V.-M. Väänänen (Eds.), *Jahtimailla: Riistalinnut* (p. 81). Espoo: Weilin + Göös.

Nowak, R. S., & Caldwell, M. M. (1984). A test of compensatory photosynthesis in the field: Implications for herbivory tolerance. *Oecologia*, *61*, 311–318.

Pennings, S. C., & Callaway, R. M. (1996). Impact of a parasitic plant on the structure and dynamics of salt marsh vegetation. *Ecology*, *77*, 1410–1419.

Pennings, S. C., & Callaway, R. M. (2002). Parasitic plants: Parallels and contrasts with herbivores. *Oecologia*, *131*, 479–489.

Press, M. C., & Phoenix, G. K. (2005). Impact of parasitic plants on natural communities. *New Phytologist*, *166*, 737–751.

Price, P. W., Westoby, M., Rice, B., Atsatt, P. R., Fritz, R., Thompson, J. N., et al. (1986). Parasite mediation in ecological interactions. *Annual Review of Ecology and Systematics*, *17*, 487–505.

Puustinen, S., & Mutikainen, P. (2001). Host–plant–herbivore interactions: Implications of host cyanogenesis. *Ecology*, *82*, 2059–2071.

Puustinen, S., & Salonen, V. (1999). The effect of host defoliation on hemiparasitic–host interactions between *Rhinanthus serotinus* and two *Poa* species. *Canadian Journal of Botany*, *77*, 523–530.

Ryttäri, T., Rautiainen, V.-P., Kemppainen, E., & Alanen, A. (2001). Putkilokasvit. In J. Ilmonen, T. Ryttäri, & A. Alanen (Eds.), *Finnish plants and invertebrate animals in the EU Habitats Directive. A scientific evaluation of the Finnish Natura 2000—proposal. The Finnish environment*. Helsinki: Finnish Environment Institute.

Siira, J., & Merilä, E. (1985). *Puccinellia phryganodes* (Poaceae) in Finland: Occurrences and ecology up to 1983. *Annales Botanici Fennici*, *22*, 281–290.

Siira, J., & Merilä, E. (1997). Rönsysorsimon esiintymät ja hoitokokeilut Suomessa vuonna 1996. The occurrence and management experiments of *Puccinellia phryganodes* in Finland 1996. *Publications of Bothnian Bay Research Station*, *10*, 1–28.

Smith, D. (2000). The population dynamics and community ecology of root hemiparasitic plants. *American Naturalist*, *155*, 13–23.

Snogerup, B. (1982). Host influence on northwest European taxa of *Odontites* (Scrophulariaceae). *Acta Botanici Fennici*, *19*, 17–30.

Snogerup, B. (1983). Northwest European taxa of *Odontites* (Scrophulariaceae). *Acta Botanici Fennici*, *124*, 1–62.

Sørensen, T. (1953). A revision of the Greenland species of *Puccinellia* parl. *Meddelar om Grønland*, *136*, 1–179.

Stowe, K. A., Marquis, R. J., Hochwender, C. G., & Simms, E. L. (2000). The evolutionary ecology of tolerance to consumer damage. *Annual Review of Ecology and Systematics*, *31*, 565–595.

Vartiainen, T. (1980). Succession of island vegetation in the land-uplift area of the northernmost Gulf of Bothnia, Finland. *Acta Botanici Fennici*, *115*, 1–105.

Vermeer, M., & Kakkuri, J. (1988). Land uplift and sea level variability spectrum using fully measured monthly means of tide gauge readings. *Finnish Marine Research*, *256*, 3–76.

Widén, K. G. (1971). The genus *Agrostis* L. in eastern Fennoscandia. Taxonomy and distribution. *Flora Fennica*, *5*, 1–209.