ANTAGONISTIC INTERACTIONS BETWEEN PLANT COMPETITION AND INSECT HERBIVORY

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Abstract. Interspecific competition between plants and herbivory by specialized insects can have synergistic effects on the growth and performance of the attacked host plant. We tested the hypothesis that competition between plants may also negatively affect the performance of herbivores as well as their top-down effect on the host plant. In such a case, the combined effects of competition and herbivory may be less than expected from a simple multiplicative response. In other words, competition and herbivory may interact antagonistically. In a greenhouse experiment, *Poa annua* was grown in the presence or absence of a competitor (either *Plantago lanceolata* or *Trifolium repens*), as well as with or without a *Poa*-specialist aphid herbivore. Both competition and herbivory negatively affected *Poa* growth. Competition also reduced aphid density on *Poa*. This effect could in part be explained by changes in the biomass and the nitrogen content of *Poa* shoots. In treatments with competitors, reduced aphid densities alleviated the negative effect of herbivory on above- and belowground *Poa* biomass. Hence, we were able to demonstrate an antagonistic interaction between plant–plant interspecific competition and herbivory. However, response indices suggested that antagonistic interactions between competition and herbivory were contingent on the identity of the competitor. We found the antagonistic effect only in treatments with *T. repens* as the competitor. We conclude that both competitor identity and the herbivore's ability to respond with changes in its density or activity to plant competition affect the magnitude and direction (synergistic vs. antagonistic) of the interaction between competition and herbivory on plant growth.

Key words: antagonistic interactions; aphids; insect herbivory; Plantago lanceolata; *plant competition;* Poa annua; Rhopalosiphum padi; Trifolium repens.

INTRODUCTION

Compared to vertebrate grazers, herbivory by insects has rather subtle effects on the structure and dynamics of plant communities (Crawley 1989). Rather than killing the whole plant, insects affect plant growth and fecundity and can thereby affect the competitive ability of the attacked plant (see Crawley 1997). Herbivore-induced shifts in the competitive hierarchy of plant species are often invoked to explain the effects of herbivorous insects on the structure and dynamics of plant communities (Carson and Root 1999, Fraser and Grime 1999, Schädler et al. 2004). The ability of a plant to capture resources for regrowth and herbivore defense depends on the competitive regime. As a result, it is often assumed that plant species that are selectively attacked by herbivores move to a lower rank in the competitive hierarchy compared to their unaffected neighbors (Crawley 1997). However, this view ignores the possibility that the effects of plant–plant interspecific

competition and insect herbivory may interact antagonistically. Antagonistic interactions of this sort would lead to the combined effects of competition and herbivory on plant growth being less than expected from a simple multiplicative model.

Although the literature on the importance of competition and insect herbivory is extensive, the mechanisms modulating the interaction between competition and herbivory are still poorly understood (Fowler and Rausher 1985, Cottam et al. 1986, Rees and Brown 1992). Hambäck and Beckerman (2003) suggested two major routes for the interaction of interspecific competition between plants and herbivory. First, the density and identity of competing plant species may affect the intensity of herbivory on a particular plant species. In "associational resistance," for example, herbivory in the presence of competing plant species may be less severe than in situations without competitors (Tahvanainen and Root 1972, Andow 1991). Secondly, competition between plant species may increase the effect of herbivory by limiting the ability of an attacked plant to compensate for losses caused by herbivores and/or by limiting the ability of the attacked plant to invest in defense. For example, a number of studies have shown a correlation between the overall impact of leaf herbivory and the intensity of competition (e.g., Windle and Franz

1979, Lee and Bazzaz 1980, Parker and Salzman 1985, Cottam et al. 1986). Several studies have documented a proportional reduction in plant growth equivalent to the product of the proportional growth under competition and herbivory alone (Fowler and Rausher 1985, Rees and Brown 1992, Willis et al. 1998), and some authors have suggested that this multiplicative interaction is the most common type of interaction between competition and herbivory (e.g., Sheppard 1996). However, the interpretation of previous studies on the interaction between competition and herbivory is hampered by the inconsistent use of raw vs. log-transformed data. Deciding if there is an interaction between herbivory and competition may depend on the scale of data. Following Rees and Brown (1992), competition affects per-gram growth rates and herbivory affects per-gram loss rates. If the two factors work independently, the joint effect should be multiplicative and therefore additive on a logarithmic scale. A significant interaction between the two factors on a linear scale would therefore not necessarily indicate a biologically meaningful interaction. Thus we follow the opinion of Rees and Brown (1992) that the multiplicative scale is more appropriate.

There are two major approaches to the study of interactions between herbivory and competition. The details of the experimental method used may determine the observed direction of the interaction between competition and herbivory (Haag et al. 2004). Some authors investigated the direct and indirect effects of herbivory by removing herbivores from both the focal plants and their competitors at the same time (Parmesan 2000, Haag et al. 2004). The relatively few studies that have used such "diffuse" herbivory treatments (meaning that it is not known which plants are directly affected by the herbivores) consistently demonstrate an antagonistic interaction between competition and herbivory. There are two mutually nonexclusive explanations for this finding. (1) The antagonistic interaction occurs because of a lower probability of the focal plant being attacked if neighbor plants are present. Thus, the intensity of herbivory on the focal plant is reduced. (2) The antagonistic interaction occurs because of a reduced intensity of competition with herbivory on *all* plants (Haag et al. 2004). In such cases, the focal plant benefits from competitive release. A more common experimental approach investigates the effects of (mostly specialized) herbivores and competition by herbivore-free plant species on the host plant. Such studies generally report multiplicative or synergistic effects (Fowler and Rausher 1985, Parker and Salzman 1985, references in Haag et al. 2004), since the effects of herbivory and competition may be simply additive or may result in a cumulative stress (Maschinski and Whitham 1989). Haag et al. (2004) suggested that studies with a single specialized herbivore are not relevant for natural systems, where most or all plant species are attacked by herbivores. By attacking dominant plant species, however, specialized

herbivores may influence the structure and dynamics of natural plant communities (Carson and Root 2000, Schädler et al. 2004).

Insect herbivores are affected by the nutritional quality of the plant material they consume (e.g., Mattson 1980, Awmack and Leather 2002, Schädler et al. 2003). This is especially true for aphids, which depend on soluble amino acids in the phloem (Van Emden 1966, Van Emden and Bashford 1969, Dixon 1985, Prosser and Douglas 1992). The competitive regime within a plant community may influence plant growth, nutrient uptake, and ultimately the nutritional quality of the plant's tissue and phloem for the plant's herbivores. The competitive regime may thus influence herbivore population growth, and, in contrast to the common expectation, competition and herbivory may show antagonistic interactions even if the competitors are not attacked. However, most studies on this topic are rather phytocentric and ignore the measurement of the herbivore population and possible effects on host plant quality. This leads to a deficit in understanding of the underlying mechanisms of these interactions.

Our study had two aims. First, we experimentally evaluated the interacting effects of plant competition and herbivory on the growth of a focal plant. We used two different plant species as competitors to examine the role of competitor identity on this interaction. We further assessed the effects of both factors on the carbon and nitrogen content of the focal plant. Second, we explored whether the type and magnitude of the interaction between interspecific competition and herbivory can be explained by changes in herbivore density. As herbivores, we used aphids, which are known to reproduce differently depending on the nutritional status of their host plants.

METHODS

Experimental design

We established a greenhouse experiment with three plant species. All three species are widely distributed across Central Europe and frequently occur together in both native grasslands and artificial meadows. *Poa annua* (L.) was used as the host species for the herbivore and was present in all experimental units. The nitrogen-fixing legume *Trifolium repens* (L.) and the herb *Plantago lanceolata* (L.) were used as competitors. In a factorial design we added the bird-cherry aphid *Rhopalosiphum padi* (L.) (Homoptera: Aphididae). This aphid species is heteroecious and holocyclic with sexual stages. It shows host plant alternation with *Prunus padus* (L.) as primary and various grasses as secondary hosts (Lehtonen et al. 2005). *Poa annua* is one of its natural hosts and the only host in the species pool of our experiment. *R. padi* is thus a "specialist" herbivore in the context of our experiment.

In April 2004, seeds of the three plant species (obtained from Rieger Hofmann GmbH, 74572 Blaufelden-Raboldshausen, Germany) were sown into pots

TABLE 1. Response indices used to assess the separate and combined effects of herbivory and competition on the growth of *Poa annua* (see *Methods*).

Response index	Formula
Herbivory response (HR)	HR = dm [with herbivores]/dm [without herbivores]
Competitive response (CR)	CR = dm [with competition]/dm [without competition]
Total response predicted (TR_{pred})	TR_{pred} = HR × CR
Total response observed (TR_{true})	TR_{true} = dm [with herbivores and competition]/dm [without herbivores and competition]

Note: dm = dry mass.

in the greenhouse. Day length was maintained at 12 hours, with additional light supplied by high-pressure sodium lamps (Philips Son-T Agro, 400 W, Monsees and Company, Sacramento, California, USA). Temperature varied between 15°C during the night and a maximum of 28°C during the day. After three weeks, seedlings were transplanted into the experimental pots (9 cm diameter and height) filled with standard potting soil (N_{min} 350 mg/L, P_2O_5 350 mg/L, K_2O 450 mg/L) and sand (1:1 volume : volume ratio). Using *Poa annua* as our target plant, three competition regimes were established: (1) no competition (one individual of *P. annua*), (2) competition with *Trifolium repens* (one plant of each species), and (3) competition with *Plantago lanceolata* (one plant of each species). We did not include a treatment with a second *Poa* plant as competitor, since the study focuses on interspecific competition with plants that should not be attacked by the herbivore. Six weeks after planting the experimental pots, two aphid nymphs per pot were added to half of the pots. All pots were enclosed with nylon gauze (200-μm mesh) to prevent the aphids from escaping. All six possible treatment combinations were replicated 18 times (total of 108 pots). To account for possible effects of environmental heterogeneity within the greenhouse, the experimental pots were randomly assigned to nine blocks with two replicates within each block. All pots were irrigated every 2–3 days with 50–100 mL of water.

The aboveground biomass of each plant was harvested after three weeks. We also removed and washed the roots of each plant in order to estimate belowground biomass of each species. Plant material was dried at 60°C to constant mass in separate paper bags. Above- and belowground biomass were subsequently weighed to the nearest 0.1 mg. Additionally, shoots of *Poa annua* were ground in a mill, and three subsamples of each individual were analyzed for carbon and nitrogen content using an Elementar Vario EL element analyzer (Elementar Analysengeräte GmbH, Hanau, Germany). For further analyses we averaged these data across subsamples.

According to Lehtonen et al. (2005), three weeks are sufficient to measure aphid population growth. Hence, after three weeks aphids were removed from the plants with a brush and stored in alcohol. In some samples the aphid populations had increased to such an extent that we decided to estimate numbers of aphids. For this we spread aphids evenly on a Petri dish and counted the number of aphids within a minimum of five 1-cm^2 squares. (We counted a minimum of 20 individuals.) The total number of aphids was then estimated by extrapolating counts to the total area of the Petri dish.

Statistical analyses

Prior to analysis, all biomass data were log-transformed to achieve normal distribution of residuals. The fact that both competition and herbivory change the rates of growth and tissue loss also suggests log-transformation of the data during analysis (Rees and Brown 1992). Element concentrations were arcsine square-root transformed and numbers of aphids were square-root transformed.

The effects of block, aphids, and competition on *P. annua* growth and the carbon and nitrogen content of the shoots were analyzed by a three-way ANOVA. Relative allocation to root biomass was analyzed, with root biomass as the response variable and shoot biomass as a covariate. The effects of block and competition on aphid density were tested using a two-way ANOVA. To remove possible confounding effects of host plant biomass and nitrogen content on aphid density, we included these variables as covariates. Note that the factor competition has three levels: none, with *Plantago,* and with *Trifolium*. When the effects of competition or the competition × herbivory interaction were significant, we used linear contrasts to determine the overall magnitude of the effect of having a neighbor present and its interaction with herbivory. The effects of block and aphid presence on the growth of *P. lanceolata* and *T. repens* were also tested using a two-way ANOVA. In all analyses, interactions with the factor block were pooled into the error term (Newman et al. 1997). ANOVAs with significant effects were followed by post hoc tests to examine further differences between treatment means (Tukey's hsd, STATISTICA 6.1, StatSoft, Tulsa, Oklahoma, USA).

To investigate the effects of herbivory and competition on growth of *P. annua* in more detail, we calculated four response indices for the aboveground biomass of *P. annua* (Haag et al. 2004) within each block (Table 1). These measures were used to test the effects of each factor in the absence and the presence of the other factor separately and to compare the combined effects of the factors with the null model. The null model was that competition and herbivory do not interact and should show a multiplicative response on the linear scale. We

TABLE 2. ANOVA results (F values) of the effects of block, competition, and herbivory on the total, shoot, and root biomass (g) and relative root allocation (root biomass per unit shoot biomass) of the focal plant *Poa annua*.

Source of variation	df	Total	Shoots	Roots	df	Relative root allocation
Shoot biomass					1	**25.05*****
Block	8, 79	1.01	1.22	0.97	8, 78	1.44
Competition (C)	2, 79	**38.57*****	**46.91*****	**9.40*****	2, 78	**4.71***
Herbivory (H)	1, 79	**58.24*****	**55.61*****	**33.13*****	1, 78	3.31
$C \times H$	2, 79	**5.41****	**4.80***	**5.91****	2, 78	2.22

Notes: Values in boldface type represent significant effects.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

calculated the herbivory response (HR; Table 1) for each competitive regime and the competition response (CR; Table 1) for treatments with and without herbivory. Since values for competition with *Plantago* and *Trifolium* refer to the same control, these indicators were analyzed separately. Values for HR or CR = 1 indicate no effect of competition or herbivory on plant growth; values <1 indicate negative effects and values >1 positive effects. These indices, however, ignore interactions of competition and herbivory (see Haag et al. 2004 for discussion). Therefore, a predicted (TR_{pred}) and observed total response index (TR_{true}) was calculated for *P. annua* in each block (Table 1). TR_{pred} indicates plant growth if competition and herbivory together had simple multiplicative effects, whereas TR_{true} is the observed effect of the combined influence of both factors. $TR_{pred} > TR_{true}$ indicates that the interaction is synergistic, $TR_{pred} < TR_{true}$ indicates that the interaction is antagonistic, and $TR_{true} = TR_{pred}$ indicates that there is no interaction between competition and herbivory (Reader and Bonser 1998, Haag et al. 2004). These response indices were log-transformed and all statistical analyses were performed on the resulting log response ratios (Hedges et al. 1999). CR and HR were analyzed by means of a two-way ANOVA, with block and herbivory (CR) or competition (HR) as factors. TR was also analyzed using a two-way ANOVA with block and "method of calculation" (predicted vs. true) as factors. An interaction between herbivory and competition is indicated by a significant value for the "method of calculation" factor.

RESULTS

Plant biomass

Both competition and herbivory reduced the growth of *Poa* (Table 2, Fig. 1). Furthermore, plant competition and herbivory showed statistically significant interacting effects on the combined and separate biomass of shoots and roots of *Poa*. Growing with neighbors had a generally negative effect on total biomass of *Poa* (linear contrast, $F_{1,79} = 65.87$, $P < 0.001$). Compared to *Poa* grown alone in the absence of herbivory, competition with *P. lanceolata* reduced mean total *Poa* biomass by 58%, and competition with *T. repens* reduced mean total *Poa* biomass by 42%. With herbivores the effects were

weaker, with the mean total biomass of *Poa* reduced by 46% in competition with *P. lanceolata* and reduced by 22% in competition with *T. repens*. Accordingly, the negative effect of having a neighbor was significantly weaker with herbivory (linear contrast, $F_{1,79} = 10.77$, $P = 0.002$). Shoot biomass of *Poa* was significantly decreased by the presence of neighboring plants (linear contrast, $F_{1,79} = 75.0$, $P < 0.001$). Without competitors, herbivores decreased shoot biomass of *Poa* by 48% and belowground biomass by 58%. This negative impact on shoot biomass was less pronounced with competitors. Herbivory reduced shoot biomass of *Poa* by 34% when *Poa* grew with *Trifolium,* and by 43% when *Poa* grew with *Plantago* (Fig. 1, linear contrast for the interaction aphids × neighbor present, $F_{1,79} = 9.60$, $P < 0.001$). Without herbivores, both competitors decreased belowground biomass by 40% compared to *Poa* growing alone in the absence of herbivores (Table 2, Fig. 1, linear contrast, $F_{1,79} = 18.31$, $P < 0.001$). However, the negative impact of herbivores on root biomass was again significantly weaker in the treatments with competitors. Compared to *Poa* growing alone in the absence of herbivory, herbivory reduced root biomass of *Poa* by 39% when *Poa* grew with *Trifolium,* and by 24% when *Poa* grew with *Plantago* (Fig. 1). Competitors thus alleviated the negative effect of the herbivore on above- and belowground biomass of *Poa* (significant competition × aphids interaction; Table 2, Fig. 1, linear contrast for the interaction aphids × neighbor present, $F_{1,79} = 11.41$ $P = 0.001$). Relative investment in root biomass was affected only by competition (Table 2, Fig. 1). Root biomass per unit shoot biomass was highest for *Poa* grown with *Plantago* and lowest for *Poa* growing with *Trifolium*. Accordingly, the effect of having a neighbor was not significant (linear contrast, $F_{1,78} = 0.001$, $P > 0.3$). Neither above- nor belowground competitor biomass was affected by herbivory on *Poa* (ANOVA, all $P > 0.05$).

Element contents

Competition did not affect the concentration of nitrogen and carbon in *Poa* shoots (Table 3). Herbivory by aphids decreased nitrogen and carbon concentrations, and we found a marginally significant interaction between competition and herbivory. Although herbivory
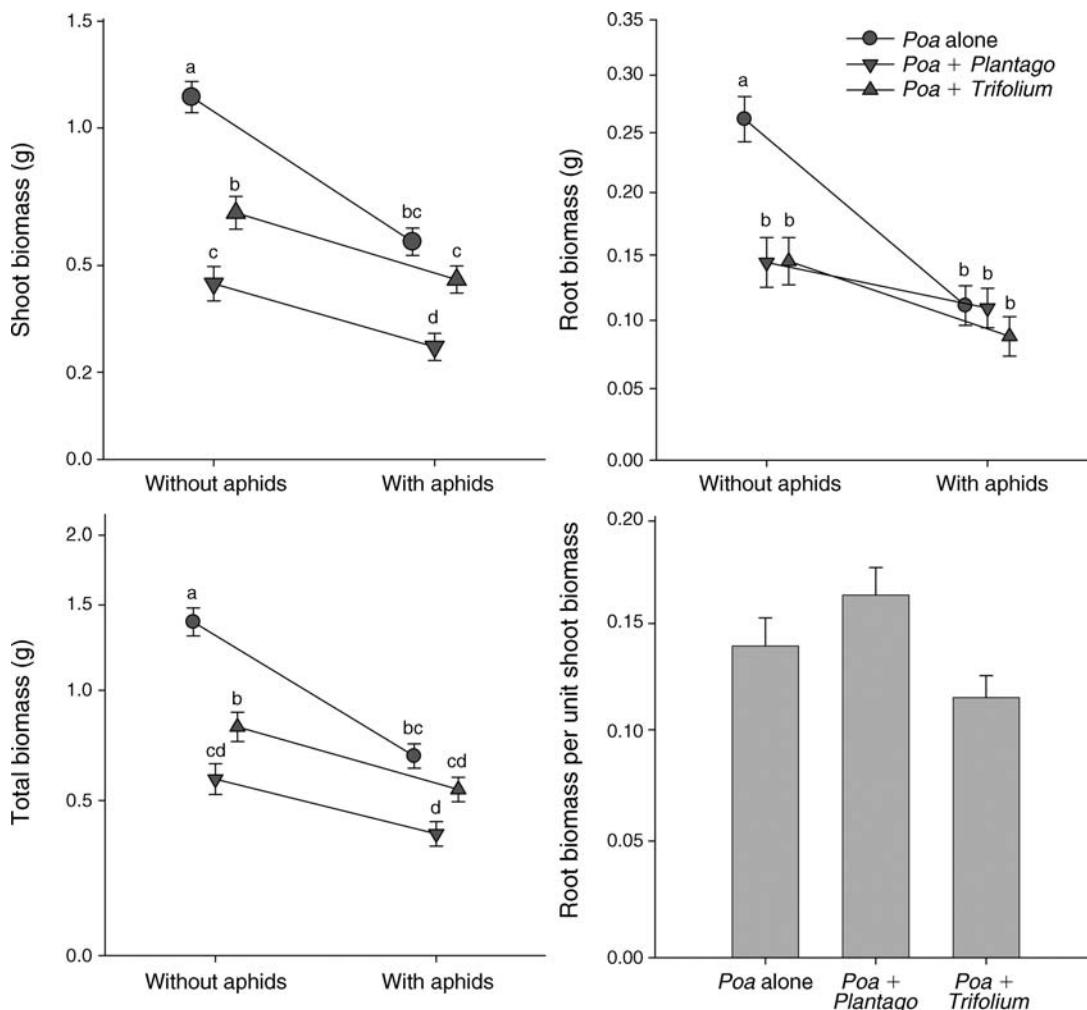
FIG. 1. Interaction plots of the biomass of *Poa annua* (mean ± SE) with and without aphid herbivory and root allocation in the different competition treatments. Different letters indicate significant differences between means following the post hoc test (Tukey's, *P* < 0.05). Note that the *y*-axes for shoot biomass, root biomass, and total biomass are on a log scale.

decreased the nitrogen content of *Poa* tissue by 11% in treatments without competition, and by 10% in treatments with *Trifolium*, herbivory did not affect nitrogen content in treatments with *Plantago* (linear contrast for the interaction aphids × neighbor present, $F_{1,79} = 1.86$, $P = 0.18$). In contrast, carbon concentration of shoots decreased by ~3% only if *Poa* was grown alone or with *Plantago* as the competitor, and was unaffected if *Poa* was grown with *Trifolium* (Fig. 2, linear contrast for the interaction aphids × neighbor present, $F_{1,79} = 0.05$, $P > 0.3$). Thus, even if the identity of the competitor affected herbivory-induced changes of element concentrations, there was no general effect of having a neighbor on these variables.

Competition and herbivory

The herbivory response (HR) of aboveground *Poa* biomass was significantly lower than 1 across the three competition treatments (*t* test against the expectation of

1; all $P < 0.008$), indicating that the presence of herbivores decreased plant growth across all three treatments. However, HR was not statistically different between the treatment without competitor and the treatment with *Plantago* as the competitor (ANOVA, $P = 0.30$). Thus, the effect of herbivory was less important if *Poa* was associated with *Trifolium* (ANOVA, $P = 0.04$,

TABLE 3. ANOVA results (*F* values) of the effects of block, competition, and herbivory on element contents in the aboveground biomass of the focal plant *Poa annua*.

Source of variation	df	Nitrogen (%)	Carbon (%)
Block	8, 79	**1.80**†	**3.75*****
Competition (*C*)	2, 79	0.74	0.50
Herbivory (*H*)	1, 79	**21.63*****	**19.04*****
C × *H*	2, 79	**2.45**†	**2.45**†

Notes: Values in boldface type represent significant effects.
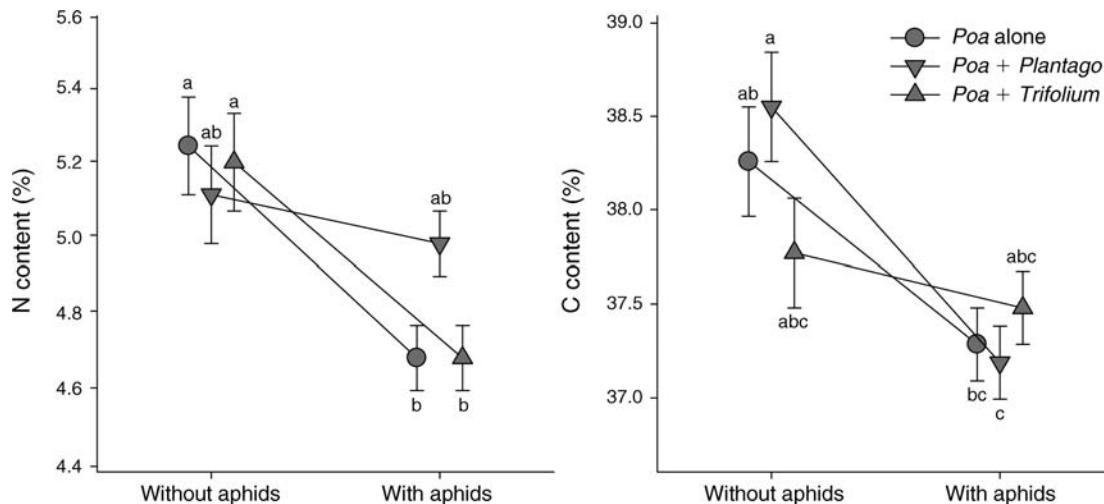† *P* < 0.1; *** *P* < 0.001.

FIG. 2. Element concentrations in the shoots of *Poa annua* (mean ± SE) with and without aphid herbivory in the different competition treatments. Different letters indicate significant differences between means following the post hoc test (Tukey's, $P < 0.05$). Note that the *y*-axes are on an arcsine square-root scale.

Fig. 3). The presence of *Trifolium* thus alleviated the negative effect of herbivory. Similarly, the competition response (CR) of aboveground *Poa* biomass was always significantly <1 (*t* test, $P \leq 0.002$). This indicates a general negative effect of competition independent of herbivory and competitor identity (Fig. 3). However, the negative effect of competition was weaker when *Poa* grew together with *Trifolium*. With aphids, the effect of competition increased significantly only in the treatment with *Trifolium* (ANOVA, $P = 0.007$; treatment with *Plantago* ANOVA, $P > 0.3$). Further, competition and herbivory only showed an antagonistic interaction when *Trifolium* was the competitor: total response (TR) of aboveground biomass of *Poa* was significantly weaker in the combined treatment than predicted from the isolated effects (ANOVA, with *Trifolium*, $P = 0.04$; with *Plantago*, $P > 0.3$, Fig. 3).

Density of herbivores

Competition decreased aphid density on *Poa* (AN-OVA, competition: $F_{2,43} = 27.2$, $P < 0.0001$). The decrease in density, however, was contingent on competitor identity (*P. lanceolata*: decrease of aphid density by 60–70%; *T. repens*: decrease by 30%; Fig. 4). The influence of competitors may be explained by the decrease of host biomass as well as by changes in the nutritional status of *Poa*. Therefore, we correlated the numbers of aphids to the aboveground biomass and nitrogen as well as carbon concentration in shoots of *Poa*. As expected, the number of aphids increased with aboveground grass biomass ($r^2 = 0.45$, $P < 0.001$), and decreased with nitrogen concentration in shoots of *Poa* ($r^2 = 0.13$, $P = 0.007$). However, using biomass and nitrogen concentration as covariates did not change our finding that the density of aphids decreased with competitors.

DISCUSSION

Our experiment showed clear negative effects of interspecific plant competition and herbivory on the growth of *Poa annua*. In contrast to the study of Haag et al. (2004), both factors had approximately the same effect. Aboveground biomass of *Poa* decreased more in competition with *Plantago* than with *Trifolium*. Competition between plants has been reported to result in an increased allocation of resources to roots (e.g., Tilman 1988, Gersani et al. 2001). In our study, however, the relative root biomass of *Poa* growing alone ranged between the two values in the competition treatments with neighboring plants. Relative investment in root biomass was highest with *Plantago* and lowest with *Trifolium*, possibly because *Poa* and *Trifolium* competed for light and not for nutrients. The response of root biomass to aboveground herbivory varies between studies. While some studies find that aboveground herbivory reduces root biomass (Ruess 1998, Mikola et al. 2001), others find no effect (McNaughton et al. 1998). However, infestations with aphids seem to reduce root biomass of the host plant (Choudhury 1984, Inbar et al. 1995). In our study, herbivory by aphids did not affect relative allocation of biomass to roots or shoots. Although we found that aphids reduced *Poa* shoot and root biomass, this did not positively affect competitor biomass.

Interspecific plant–plant competition negatively affected aphid population growth in our experiment. Although we have no direct data on the nutritional quality of the phloem sap, circumstantial evidence suggests that competition influences the nutritional status of the host plant. First, the number of aphids declined with decreasing shoot biomass of *Poa*, although an alternative explanation for this observation could be the decreased number of suitable feeding sites. Second,
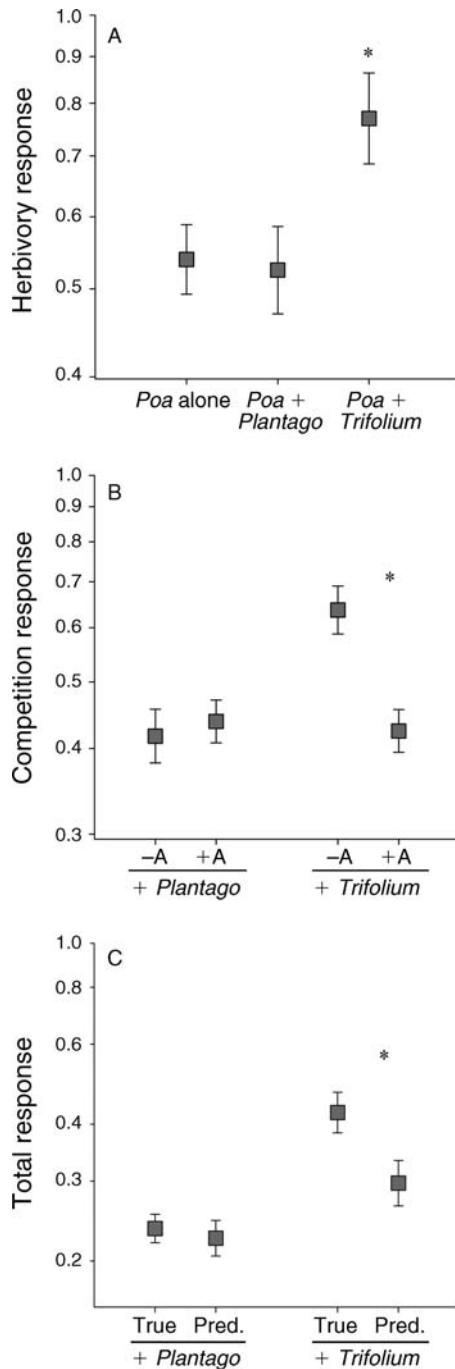
FIG. 3. (A) Herbivory response, HR, defined as (plant dry mass with herbivores) ÷ (plant dry mass without herbivores), as a function of competition treatment; (B) competition response, CR, defined as (plant dry mass with competition) ÷ (plant dry mass without competition) as a function of competing plant species and aphid herbivory (−A, without aphids; +A, with aphids); and (C) total response as a function of the method of calculation (true and pred. [predicted]). Asterisks indicate significant differences between (A) herbivory response in the respective competition treatment and the control; (B) competition responses with and without aphids according to competition treatment; (C) methods of calculation of total responses according to competition treatment (means ± SE). Note that the y-axes are on a log scale.

the impact of competitors on herbivores was contingent on competitor identity. We found that *Trifolium* had much less impact on aphid density than did *Plantago*, perhaps because the ability of *Trifolium* to fix nitrogen reduces the intensity of competition for this nutrient.

The nitrogen content in *Poa* shoots decreased with increasing number of aphids, indicating that aphids act as sinks for nutrients. Phloem nutritional quality, however, is often poorly related to the quality of leaf tissue (Dixon 1985). Hale et al. (2003) showed that water stress in host plants (e.g., as a consequence of plant competition) reduced the ingestion of amino acids by aphids, which negatively affected the performance of *R. padi*. Nevertheless, an adequate supply of a balanced diet containing certain essential amino acids is crucial for aphid survival and reproduction (Prosser and Douglas 1992). Thus, changes in the quality rather than quantity of nitrogen-based compounds in the phloem may explain the differences in aphid performance (Van Emden 1966, Van Emden and Bashford 1969, Dixon 1985). There is still a considerable lack of knowledge of how plant competition may affect plant tissues and consequently herbivore performance. Future experiments need to concentrate on these aspects.

The negative effect of herbivory on total biomass and root biomass differed between the competition treatments. We found the highest effect of herbivory on *Poa* with no competitor, an intermediate effect on *Poa* in the treatment with *Plantago,* and the lowest effect with *Trifolium*. This result contrasts with the common expectation of synergistic interactions: the plant's ability to compensate for herbivory should be higher when competition for resources is low or absent. According to the response indices, *Poa* plants that grew in competition with *Trifolium* suffered less from aphid herbivory than plants growing alone or with *Plantago*. Herbivory
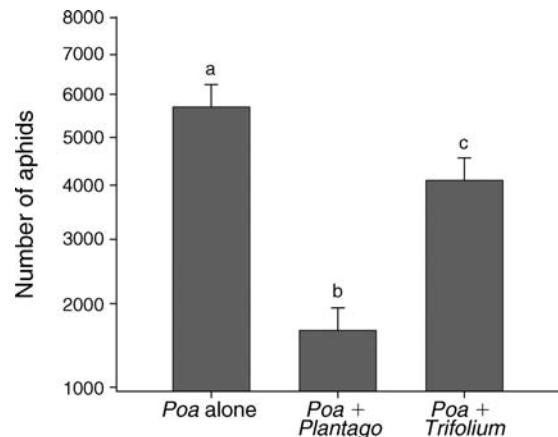

FIG. 4. Number of aphids (means + SE) on *Poa annua* according to the different competition treatments. Different letters indicate significant differences between means following the post hoc test (Tukey's, $P < 0.05$). Note that the y-axis is on a square-root scale.

by aphids also influenced the strength of competition. The reduction of biomass due to competition with *Trifolium* was stronger when aphids were present, implying that competition by *Trifolium* and aphid herbivory interacted antagonistically. In contrast, herbivory had no effects on the intensity of competition with *Plantago*.

Reader and Bonser (1998) argued that one can predict the combined effects of herbivory and competition by multiplying the individual effects of both factors, since their proportional effect may not change depending on the level of the other factor. This null model assumes that the two factors independently affect plant biomass (see also Rees and Brown 1992, Cahill 1999). On a logarithmic scale these effects would be additive. However, if herbivory also affects plant growth (e.g., as a result of a changed competitive regime), interactions with competition should be nonadditive on a logarithmic scale (Rees and Brown 1992). In this case, interactions between herbivory and competition would be synergistic, since herbivores are expected to decrease the competitive ability of an individual plant (see Crawley 1997 for review). In contrast to this expectation we demonstrated antagonistic interactions between a specialist herbivore and interspecific plant competition. We explain this fundamental difference by the negative feedback of plant competition on the performance of the herbivore. Most experiments focus on the effects of grazing or simulated herbivory (clipping). Clipping removes a constant amount of plant tissue, and, in contrast to real herbivory, shows no response to tissue quality. Hence, clipping ignores the possibility of differential performance and reproduction of herbivores on the focal plant in response to plant–plant interactions. In grazer experiments, however, herbivores often respond to diminished tissue quality with compensatory feeding (Bezemer and Jones 1998). However, this does not allow for predictions of changes in performance and reproduction in the longer term, since it has been shown that changes in the feeding rate do not necessarily translate into changes of herbivore performance traits (e.g., relative growth rate [Schädler et al., *in press*]).

Neighboring plants may affect the level of herbivory on a focal plant by a variety of mechanisms. This includes interactions with parasites and predators of the herbivore, visual and chemical masking, and effects of competitors on resistance (reviewed in Agrawal 2004). However, herbivory or competition may simply interact by influencing the ability of an individual plant to cope with the other factor. Parmesan (2000) showed that due to resource limitation, herbivory reduced plant fitness at low plant densities, but not high densities. Similarly, Meyer and Root (1993) demonstrated that low resource conditions (which may also be caused by high competition intensity) prevented herbivores from decreasing goldenrod seed set. This finding is supported by our experiment, where the effect of the herbivore was lower with competition than without competition. However,

by means of biomass reduction *Plantago* had obviously strong competitive effects on our focal plant. At the same time aphids had an intermediate effect on shoot biomass of *Poa* growing with *Plantago*. This may be explained by the confounding effect of aphid reproduction on plants growing in a different competitive environment. Offspring number was reduced most strongly under competition with *Plantago*, which in turn may have decreased their relative effects on plant growth. We therefore conclude that these effects differ from what one would find if intensity of herbivory was kept at a constant level. Changes in herbivore reproduction can thus influence both the magnitude and direction of interacting effects between competition and herbivory.

CONCLUSIONS

The effect of herbivory and interspecific plant competition on a focal plant have been suggested to be multiplicative or synergistic when herbivory is restricted to the focal plant, or to be antagonistic if herbivory affects all of the plants within the community. In contrast, we showed that even in experiments with herbivory restricted to the focal plant, competition and herbivory interact antagonistically as long as interspecific plant competition decreases the population growth of herbivores on the focal plant. If competition between plants decreases antiherbivore defense or the ability to regrow, multiplicative or synergistic effects are expected. Hence, ecological details like competitor identity and the ability of the herbivore to respond to changed tissue quality determine the direction of the interactions between competition and herbivory.

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