

Does plant competition intensity rather depend on biomass or on species identity?

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Abstract

In two experiments, we tested whether species specific traits or mainly biomass determines the competitive strength of plant individuals in resource-poor habitats. As measure of competition intensity, we calculated the log Response Ratio (lnRR) based on total biomass for three key species of early successional stages on inland dunes. Using seedlings of *Corynephorus canescens* and *Hieracium pilosella* in a pot experiment, competition intensity was significantly and positively correlated with the biomass of the respective competitors. In contrast, such a correlation was not detected in a controlled field experiment with adult plants of the two species and of *Carex arenaria*. However, in both experiments the strength of competitive interactions (measured as lnRR) significantly depended on the identity of the competing species. We conclude, that a biomass advantage over the competitors (which can for instance be achieved by earlier germination) seems to play a crucial role only for successful seedling establishment, while competitive interactions of neighbouring plants depend on species-specific biomass allocation strategies at both developmental stages.

Um zu testen, ob artspezifische Eigenschaften oder hauptsächlich die Biomasse selbst die Konkurrenzstärke zwischen Pflanzen auf ressourcenarmen Standorten bestimmen, wurde der Log Response Ratio (lnRR) der Gesamtbiomasse für drei dominante Arten früher Sukzessionsstadien auf Sand bestimmt. In einem Topfexperiment, in dem Keimlinge der Arten *Corynephorus canescens* und *Hieracium pilosella* verwendet wurden, nahm die Konkurrenz mit zunehmender Biomasse umgebender Keimlinge signifikant zu. In einem zweiten Experiment unter kontrollierten Freilandbedingungen, dagegen, in dem ausgewachsene Pflanzen der gleichen Arten zusammen mit *Carex arenaria* gemessen wurden, war die Konkurrenzintensität nicht signifikant von der Biomasse benachbarter Pflanzen abhängig. Artspezifische Eigenschaften hatten jedoch einen signifikanten Einfluss auf die Konkurrenzstärke sowohl von Keimlingen als auch von älteren Pflanzen. Wir folgern daraus, dass ein zeitlicher Vorsprung bei der Besiedlung offener Flächen, der mit höherer Biomasse einher geht, für einen Keimling einen entscheidenden Konkurrenzvorteil bietet. Mit zunehmendem Alter jedoch nimmt der Einfluss der Biomasse auf das Konkurrenzgeschehen ab und die artspezifische Biomasse-Allokation gewinnt mehr und mehr an Bedeutung.

Key words: *Corynephorus canescens* – *Hieracium pilosella* – *Carex arenaria* – log Response Ratio – sandy soil

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Introduction

So far many studies considered changing resource gradients in different habitats, while within one plant community or at the single plant level, the correlation of competition and biomass is much less debated. However, the change of target plant biomass with density of neighbours has been modelled (Shinozaki & Kira 1956, Mead 1979, Firbank & Watkinson 1985, Connolly 1986, Firbank & Watkinson 1990, Humphrey & Pyke 1998) and the few mathematical approaches for a conceptual integration of neighbour biomass into competition indices (Goldberg 1987, Freckleton & Watkinson 2000) reflect that density and biomass are obviously correlated. In both cases, the function between target plant growth and neighbour plant density (biomass) is generally expected to be either inverse linear or hyperbolic (see Fig. 5, Mead 1979, Firbank & Watkinson 1985, 1990, Connolly 1986, Austin et al. 1988, Humphrey & Pyke 1998), i.e. the curve shows a considerable descend at low and a rather shallow decrease at high neighbour densities.

Accordingly, competition between small plants (e.g. seedlings), or at low neighbour density, should follow a pattern, where a small increase in neighbour biomass results in a considerable decrease of target biomass. In contrast, one should expect only minimal changes of target biomass in competitive interaction between adult plants (and/or at higher neighbour density) even if neighbour biomass intensively changes. In the field, plant densities are often rather in the stages with high neighbouring biomass, which is why we hypothesise, that neighbouring species biomass might play a subordinate role in determining competition patterns in natural vegetation.

We choose three dominant and often co-occurring species of early successional stages on inland dunes to study this question with both, a pot and a field-like competition experiment. To analyse competitive strength in the target-neighbour design we used the "log Response Ratio" (lnRR) rather than the "relative competition intensity" (RCI) for mainly statistical reasons (see methods). We performed the analysis with both RCI and lnRR and found no qualitative differences between the two indices. Therefore only the lnRR will be presented.

The present study was set up to investigate, whether in a situation of existing competition the biomass of neighbouring species or rather species-specific attributes determine the competitive strength of plants coexisting in the same habitat. Therefore we analysed linear regressions of target plant lnRR on total neighbour biomass to ask, (1) whether there are significant regression slopes which indicate an effect of plant

biomass on competition intensity, and (2) whether there are different elevations of regression lines between species indicating that species-specific traits do affect competitive strength.

Materials and methods

Species description

All three study species are common plants of European coastal and inland sand dunes where they are predominantly found in the early successional stages. *Corynephorus canescens* (L.) P. Beauv. is a tufted wintergreen perennial grass that occurs on open sand. The species has a finely divided, fibrous root system without rhizome. The bulk of its roots is about 25 cm long, and the maximum length is 35–40 cm. Its roots are mainly directed downwards with only few or no horizontal ones (Marshall 1967). *Hieracium pilosella* L. (the mouse-ear hawkweed) is a stoloniferous perennial, with extended clonal growth in often denser vegetation cover. *H. pilosella* forms a fine, spiders' web like rather superficial root system with intensive lateral growth and only some thicker deep growing roots of 30 to 40 cm length (personal observation). The third species, *Carex arenaria* L. (the sand sedge) is a sympodial plant forming an extensive perennial rhizome system. *C. arenaria* is generally more abundant on dry grassland stages and sometimes open pine forests on sand. A distinctive morphological feature of the species is the root dimorphism. At the base of each shoot one or two large sinker roots emerge, together with several finer roots. Fine roots may reach about 50 cm in length and the large sinker roots may grow 2 m in one summer, while the maximum reported rooting depth for the plant was 3–4 m in deep sand (Noble 1982).

The three species are the only dominant perennials on these rather species poor stages that could be selected for their differences in growth of both above- and belowground structures, which we assumed might influence competitive patterns. Rather than forming one successional stage together, where the three are all key species, they are dominant in different but subsequent stages of succession on inland dunes. However, one can often find the species co-occurring on intermediate vegetation patches and as single plants within each others dominant stages, which is comparable to the density and ground cover in the field-like experiment with adult plants (see below). Seeds of *H. pilosella* and *C. canescens* both germinate during late summer under favourable climatic conditions often together in small disturbed patches.

Seedling competition experiment

In a pot experiment with *H. pilosella* and *C. canescens* we first tested the influence of different biomass of seedlings on competitive interactions. *H. pilosella* plants were grown from seeds collected from approximately 20 maternal plants from an area of 100 m × 20 m with patchy vegetation of all early successional stages in an inland dune area called "Senne" near Bielefeld (co-ordinates: 08° 40' E 51° 57' N). For *C. canescens* seed material from seven German botanical gardens was mixed. Subsequently, seedlings of three different age classes (10, 32 and 54 days old, respectively) were planted either alone (control) or with 4 individuals per pot (pot diameter 9 cm; pot height 7.5 cm) filled with pure sand. The competitive design was set up as two pairs of two equally aged plants, and included all combinations of species and age. Therefore, for instance, a pair of 10 days old *H. pilosella* seedlings was grown with pairs of 10, 32 and 54 days old seedlings of conspecifics and of *C. canescens* seedlings. Each treatment was replicated 5 times, totalling 105 competitive pots and 30 control pots. Within pots, the planting design was of square shape, with one plant on each corner of the square (2.1 cm). Plants will be referred to as targets (focal species) and competitors (second pair of plants, which can be the same or the other species). Note, however, that each pair of plants is both target and competitor for different treatments.

Plants were cultivated in a growth chamber at temperatures of 20/15 °C (day/night) and a 12 h light period ($550 \pm 50 \mu\text{mol PAR} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). Pots were rearranged randomly every second day. Total, i.e. above- and belowground, biomass of all plants was harvested after 8 weeks of growth in April 1999 and dried for 3 days at 70 °C. For the analysis we used sums of total biomass of the two corresponding plants in all treatments.

Adult-plant competition experiment

In the second experiment competitive interactions of adult plants were tested under more field-like conditions and for a longer period of time. All three study species were grown together in an experimental "sand pit", divided into 4 isolated chambers (each: length: 6 m, width: 5 m, depth: 1.2 m) filled with pure sand. The sand pit was built in a common garden area next to the University of Bielefeld, Germany. Plants of all species were grown from seeds collected in an inland dune area near Bielefeld (see above) and sown for germination 3 months prior to the start of the experiment. Mean total dry weight (\pm S.E.) per plant at the start of the experiment was equal for *H. pilosella* (0.38 ± 0.02 g) and *C. canescens* (0.32 ± 0.02 g) while

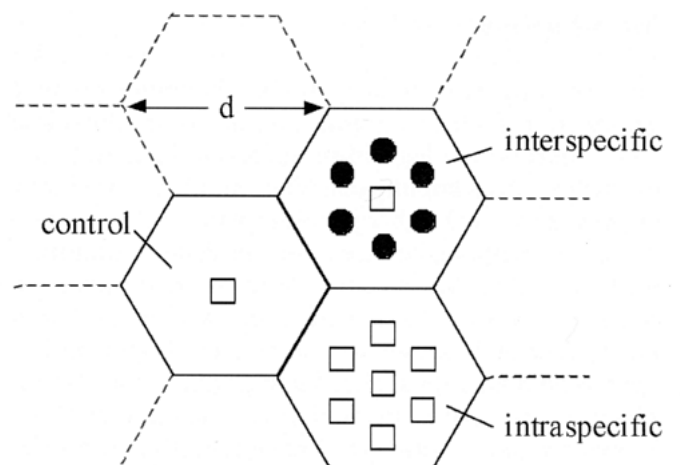


Fig. 1. Planting design of the adult-plant competition experiment. 120 hexagonal plots (diameter $d = 55$ cm, distance target-neighbour plants 7.5 cm) were established in each of four chambers of a "sand pit". Circles and squares represent different species.

C. arenaria plants were less heavy (0.13 ± 0.00 g) though equal or bigger in size. After planting from 19–22 of April 1999 plants were grown in a one-factorial complete randomised block design with water availability as variable factor. The differences in water supply (low vs. sufficient water availability) were part of a separate enquiry within the same project and will be presented in detail elsewhere. It is important to note that water availability had no particular effect in the present study, and therefore both the high and the low water treatment were included here. Single plots were planted as target-neighbour design, specifically a hexagonal design (*sensu* Gibson et al. 1999) with one target and 6 border plants (Fig. 1). Each treatment, i.e. control, intra- and interspecific competition for all species combinations, were replicated 32 times (including \pm water, i.e. 16 with high and 16 with low water). Above- and belowground biomass of all plants was harvested from 11–14 of October 1999 and dried for at least 5 days at 70 °C. All subsequent calculations are based on total biomass per plant, i.e. total dry weight per plant of all treatments.

Data analysis

To quantify competitive interaction between plants the log Response Ratio (lnRR, Goldberg et al. 1999) was calculated as

$$\ln\text{RR} = \ln(P_{\text{contr}}/P_{\text{mix}}) \quad (1)$$

where P_{contr} represents total biomass of a target plant grown alone (control) and P_{mix} represents total biomass of a target plant grown in intra- or interspecific competition. Goldberg et al. (1999) supposed the lnRR may provide a more suitable measure of compet-

itive interaction than RCI, because lnRR is symmetrical for competitive and facilitative interactions and it does not impose a ceiling on the maximum possible competition intensity. Hedges et al. (1999) favoured lnRR, because the logarithm linearises the metric and normalises the sampling distribution, that is originally skewed (but see Osenberg et al. 1999).

To differentiate between the effects of neighbour biomass and species specific effects we used regression analyses based on linear regression of lnRR of target plants on total biomass of neighbouring plants. To test for the biomass effect of competing plants the significance of slopes of regression lines was calculated. To analyse the species specific effect we used a method described by Zar (1999), where the equality of two regression coefficients (like in the seedlings experiment) involves the use of Student's *t* test (analogous to testing for differences between means). If the two regression lines do not have significantly different slopes (i.e. lines are parallel) then they can be tested for having the same elevation, again with a *t* test and the help of the so called "common" regression (essentially the sum of single regression parameters). Hence, each pair of linear regressions was compared for differences in elevation, i.e. we searched for significant differences of height (relative to the ordinate). If more than two regression lines are to be compared (like in the adult competition experiment) an analysis of covariance is used, where additional to the "common" regression a

"total" regression over the residual sum of squares of all original data points is computed (Zar 1999).

Differences between mean lnRR over all treatments were tested using ANOVA.

Results

Seedling competition experiment

Figure 2 shows the effect of mean biomass per plant of *C. canescens* and *H. pilosella* as competitors on mean target plant log Response Ratio (lnRR) for the same species of the seedling competition experiment. For all but one of the twelve regression lines the lnRR of targets significantly increased with increasing biomass of competitors (see single regression parameters in Tab. 1). Hence, intensity of competition significantly increased with biomass of competing seedlings, whether neighbouring seedlings belong to the same or the other species.

To analyse the species specific effect of competing seedlings, the pairs of linear regressions within the six diagrams of Figure 2 were compared. This analysis revealed significant differences between the elevations of the regression lines of *C. canescens* and *H. pilosella* for all age classes of seedlings, except for the oldest of *C. canescens*, where no significant differences between the two neighbouring species could be detected

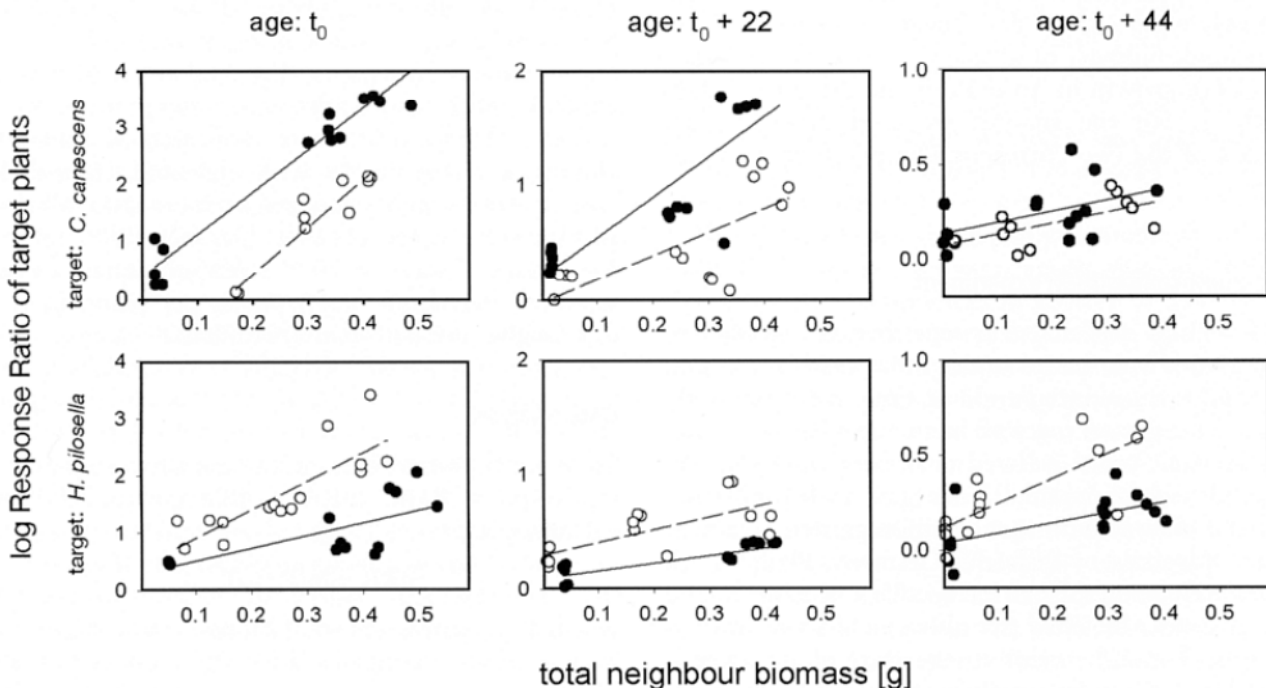


Fig. 2. Effect of total biomass of *Corynephorus canescens* (open circles) and *Hieracium pilosella* (closed circles) as competitors on the log Response Ratio (lnRR) of individual target plants of both species in the seedling competition experiment. See Table 1 for statistics.

Table 1. Analysis of neighbour biomass effects on the log Response Ratio (lnRR) of target plants of different age in the seedling experiment. "Single regression parameters" are coefficients from linear regressions of target plant lnRR on total neighbour biomass, where b is the slope of regression; values for comparison of slope and the elevation of these regression lines are given in the two right columns of the table.

	single regression parameters				slope of single regression		comparison of slope		comparison of elevation	
	r ²	b	SS	dF	F	p	t	p	t	p
target age: t₀										
<i>Corynephorus canescens</i>										
with <i>C. canescens</i>	0.94	8.32	0.64	13	213.90	<0.001				
with <i>H. pilosella</i>	0.94	7.39	1.45	13	219.24	<0.001				
Common regression*		7.63	2.19	27			1.10	>0.20	12.95	<0.001
<i>Hieracium pilosella</i>										
with <i>C. canescens</i>	0.69	4.96	2.43	13	28.41	<0.001				
with <i>H. pilosella</i>	0.56	2.21	1.87	13	16.68	<0.01				
Common regression*		3.05	5.42	27			2.62	<0.02	5.20	<0.001
target age: t₀ + 22 days										
<i>Corynephorus canescens</i>										
with <i>C. canescens</i>	0.54	2.06	1.28	13	15.19	<0.01				
with <i>H. pilosella</i>	0.73	3.51	1.53	13	35.11	<0.001				
Common regression*		2.76	3.18	27			1.83	>0.05	4.37	<0.001
<i>Hieracium pilosella</i>										
with <i>C. canescens</i>	0.52	1.12	0.39	13	14.07	<0.01				
with <i>H. pilosella</i>	0.72	0.66	0.05	13	33.38	<0.001				
Common regression*		0.88	0.48	27			1.43	>0.1	6.02	<0.001
target age: t₀ + 44 days										
<i>Corynephorus canescens</i>										
with <i>C. canescens</i>	0.51	0.59	0.09	13	13.46	<0.01				
with <i>H. pilosella</i>	0.25	0.59	0.24	13	4.23	>0.05				
Common regression*		0.59	0.33	27			0.01	>0.5	1.55	<0.01
<i>Hieracium pilosella</i>										
with <i>C. canescens</i>	0.65	1.32	2.43	13	28.41	<0.001				
with <i>H. pilosella</i>	0.35	0.54	1.87	13	16.68	<0.01				
Common regression*		0.89	5.42	27			2.32	<0.05	3.90	<0.001

* calculated parameters for the sum of residuals for both regressions

(Tab. 1, comparison of elevation). Moreover, interspecific competitive effects were generally higher than intraspecific competition for both target species. The mean lnRR \pm SE for (a) *H. pilosella* as target is 0.824 ± 0.110 with *C. canescens*, 0.458 ± 0.072 with *H. pilosella* and for (b) *C. canescens* as target: 1.179 ± 0.183 with *H. pilosella* and 0.638 ± 0.110 with *C. canescens*.

Adult-plant competition experiment

In contrast to the result for competing seedlings, no interrelation between target plant lnRR and neighbouring plant biomass was found for adult plants of *C. canescens*, *H. pilosella* and *C. arenaria* (Fig. 3). For the weak correlations between target and neighbour plants with an R² of 0.00 to 0.27 (Tab. 2), no significant differences from zero could be detected for the slopes of the regression lines (see single regression parameters in Tab. 2). The two exceptions from this rule (target *H. pilosella*; neighbour *C. canescens* and target

and neighbour *C. arenaria*) show a decline of lnRR and hence competition intensity with increasing neighbour biomass. In general, however, competition intensity between adult plants under field-like conditions did not significantly depend on the biomass of neighbouring plants.

To determine the species specific effect for the adult competition experiment, the graphs within the rows of Figure 3 were compared. The analysis revealed, that the lnRR of all three target species significantly changed with neighbouring plant species (Tab. 2, comparison of elevation and post-hoc test). This corresponds well with the results of an ANOVA of the data shown in Figure 4, which illustrates that *C. canescens* has the highest competitive effect on all target plant species, no matter whether the interaction is intra- or interspecific, followed by *H. pilosella* and *C. arenaria*. Overall, species specific traits had a significant effect on the strength of competitive interactions between both seedlings and adult plants.

Discussion

The present study was set up to answer two distinct questions that will be addressed separately in the following discussion. We will first analyse whether there was an effect of neighbour biomass on competition intensity. Then the results supporting that species-specific traits determine competitive strength will be discussed before finally we draw some general conclusions out of the comparison of both.

Biomass effect

Our results show species-specific effects on competition intensity both for seedlings and adult plants and a significant effect of competing plant biomass on the log Response Ratio (lnRR) only of target seedlings. This corresponds well with the expected hyperbolic function between target plant growth and neighbour plant density introduced earlier. As illustrated in Figure 5, competition between small plants (or seedlings) would still be in section A of the curve, where a small increase in neighbour biomass results in a considerable decrease of target plant biomass and hence an increase in lnRR – similar to what our results showed for the seedling competition experiment.

In contrast, the experiment with adult plants, where one target competes with 6 neighbours, describes region B of Figure 5 where considerable neighbour biomass changes result only in minimal changes of target biomass and, correspondingly, lnRR. It might not be surprising that region B of the curve fits the competitive relationship with *C. canescens* and *H. pilosella* both of which built up a high total neighbour biomass of 10 to 50 g dry weight. However, even though the biomass of *C. arenaria* is naturally much lower (between 0.5 and 18 g), still no significant correlation of target and neighbour performance could be detected. The two exceptions from this rule within the adult competition experiment (target *H. pilosella*; neighbour *C. canescens* and target and neighbour *C. arenaria*) even show a decline of lnRR and hence a decline of competition intensity with increasing neighbour biomass.

Still, if the scale of neighbour biomass was wider an effect of biomass on competition intensity should be detectable to some extent. Several papers so far showed a positive correlation of competition and density (Weiner 1982, 1984, Firbank & Watkinson 1985, 1990, Connolly et al. 1990, Cousens & O'Neill 1993, Freckleton & Watkinson 1997, 1999) or biomass (Goldberg 1987, Bonser & Reader 1995) of compet-

Table 2. Effects of neighbour biomass on the log Response Ratio (lnRR) of target plants of the adult competition experiment. "Parameters of single regressions" are coefficients from linear regressions of target plant lnRR on total neighbour biomass, where b is the slope of regression; Values for the comparison of slope and elevation of these regression lines are given in the two right columns of the table, calculated by means of the 'common' and 'total' regression; Different letters in the last column indicate significant differences between the elevations of corresponding regressions (post-hoc Scheffé-test; $p < 0.001$ except for target *C. canescens* where $p < 0.05$).

	single regression parameters				slope of single regression		comparison of slope		comparison of elevation		post-hoc
	r ²	b	SS	dF	F	p	F	p	F	p	
<i>Corynephorus canescens</i>											
neighbor <i>C. canescens</i>	0.00	0.00	9.19	30	0.09	0.761					a
neighbor <i>H. pilosella</i>	0.00	0.00	10.12	30	0.01	0.930					b
neighbor <i>C. arenaria</i>	0.01	-0.02	4.01	30	0.26	0.612					c
Common regression*		0.00	23.38	92							
Total regression**		0.04	33.24	94			0.10	>0.25	19.40	<0.001	
<i>Hieracium pilosella</i>											
neighbor <i>C. canescens</i>	0.25	-0.03	8.30	30	10.21	0.003					a
neighbor <i>H. pilosella</i>	0.00	0.00	16.51	30	0.03	0.876					b
neighbor <i>C. arenaria</i>	0.06	-0.03	5.73	30	1.86	0.183					c
Common regression*		-0.02	32.06	92							
Total regression**		0.04	59.39	94			2.23	>0.05	39.21	<0.001	
<i>Carex arenaria</i>											
neighbor <i>C. canescens</i>	0.01	-0.01	14.55	34	0.36	0.551					a
neighbor <i>H. pilosella</i>	0.00	-0.01	25.27	34	0.15	0.704					b
neighbor <i>C. arenaria</i>	0.24	-0.07	22.22	32	10.34	0.003					c
Common regression*		-0.02	66.63	102							
Total regression**		0.04	114.75	104			3.70	<0.05	36.84	<0.001	

* calculated parameters for the sum of residuals for both regressions

** calculated parameters for the regression over all original data points of the two regression lines to be compared

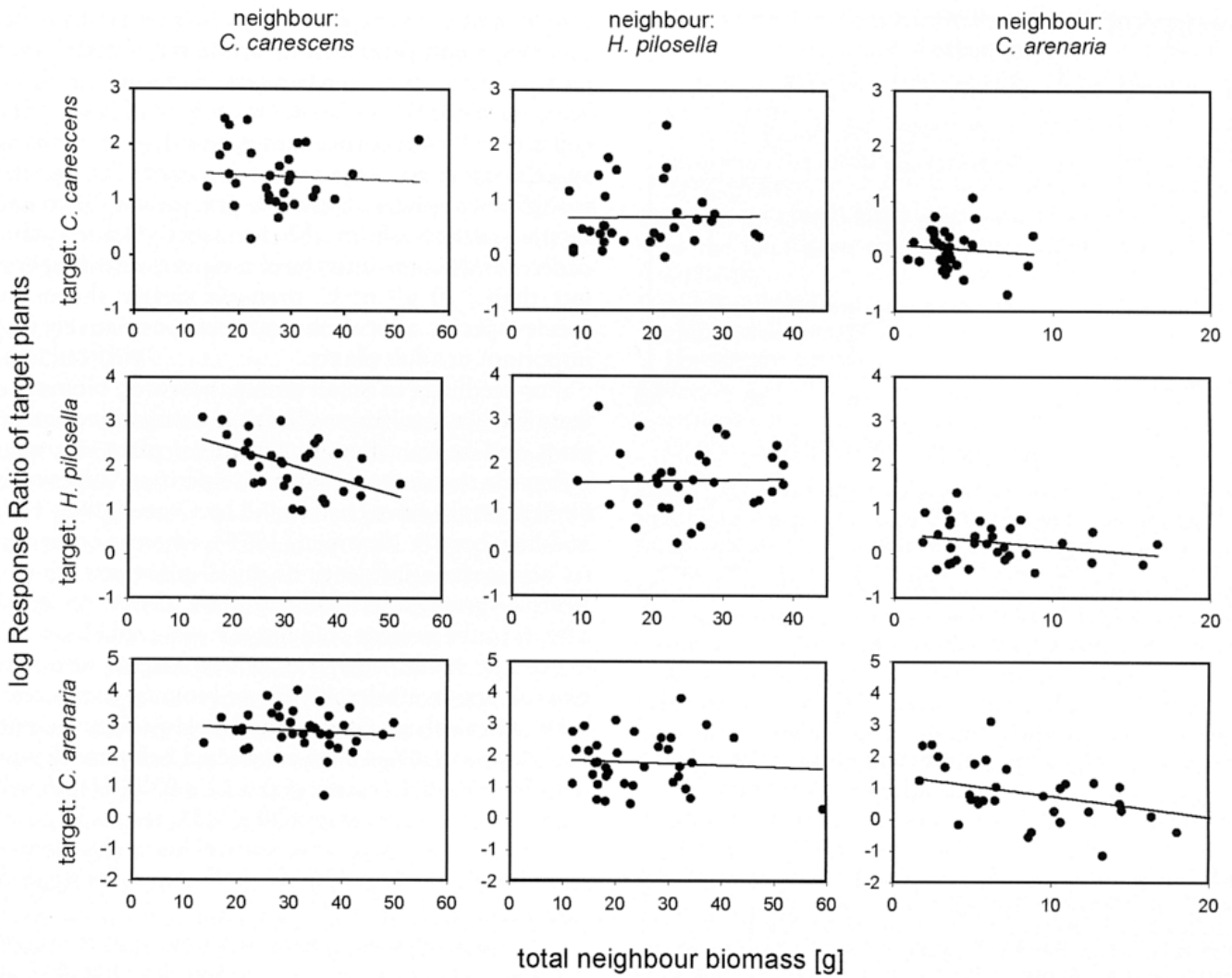


Fig. 3. Effect of total neighbours biomass on the log Response Ratio (lnRR) of individual target plants of *Corynephorus canescens*, *Hieracium pilosella* and *Carex arenaria* in the adult-plant competition experiment. Given are results for all combinations of target and neighbour species with targets arranged in columns and neighbours in rows. Note the differences in scales in the various graphs. See Table 2 for statistics.

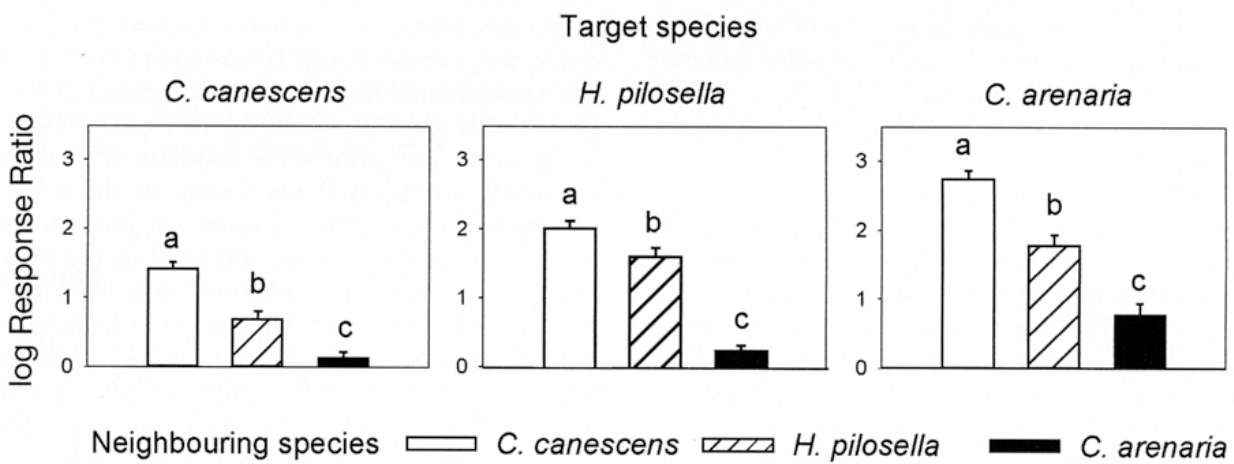


Fig. 4. Log Response Ratio for *Corynephorus canescens*, *Hieracium pilosella* and *Carex arenaria* as target (different graphs) and neighbour species (bars within graphs) in the adult-plant competition experiment. Given are means \pm S.E. over all treatments. Different letters indicate significant differences (ANOVA, post-hoc Scheffé-test, $p < 0.001$ except for plot of *H. pilosella* between *C. canescens* and *H. pilosella*, where $p < 0.05$; $n = 32$).

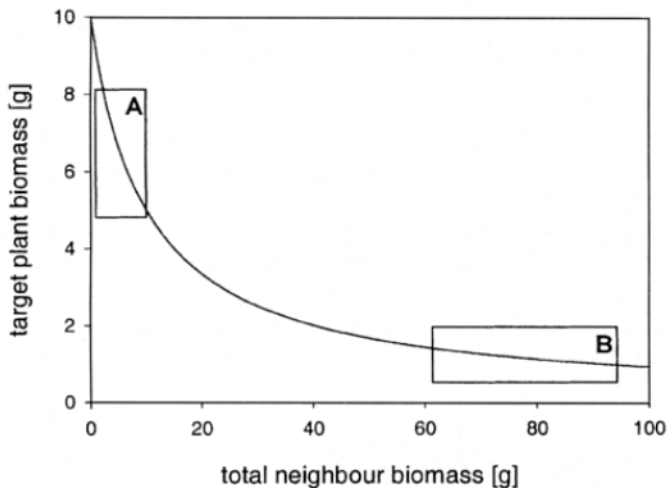


Fig. 5. Hypothesised hyperbolic relationship between target plant biomass and mean biomass of neighbouring plants ($y = y_{\max}/(1+\alpha x)$, where target biomass without competition (y_{\max}) and the fitting constant (α) are arbitrarily set to 10 and 0.1, respectively). The slope of the curve would be positive, if $\ln RR$ instead of biomass was presented for the target plant. The graph suggests high dependence of competition intensity on neighbour biomass at low biomass of neighbouring plants and vice versa.

ing species or of both parameters (Grace 1985, Goldberg & Fleetwood 1987, Goldberg & Landa 1991). On the other hand, there is also evidence, that competitive interaction does not significantly depend on neighbouring plant biomass (Berkowitz et al. 1995, Davis et al. 1998), although the latter studies worked with seedlings, where we found a relationship, as did Connolly & Wayne (1996) before. Possibly, our data do not correspond to these findings because of the selection of species.

In the present study we found that beyond the rather obvious difference of “with” and “without” competition, there was no additional effect of biomass on plant interactions between the studied species. This clearly shows that the importance of a biomass effect in determining competitive strength of plant individuals declines with age (or standing crop).

Species effect

A comparison of the elevation of regression lines to detect differences between neighbouring species revealed that species specific traits, in contrast to biomass alone, did have a significant effect on competition intensity between both seedlings and adult plants. For the latter, results of $\ln RR$ revealed a distinct competitive hierarchy with *C. canescens* > *H. pilosella* > *C. arenaria* (where “>” indicates competitive superiority). It could be supposed, however that this competitive hierarchy depended on the initial and/or general plant size, that both differed between

the studied species. The rank order of overall plant biomass equals the one of competitive hierarchy (mean biomass \pm S.E. of *C. canescens* > *H. pilosella* > *C. arenaria* with 11.27 ± 0.60 , 5.24 ± 0.39 and 2.15 ± 0.21 , respectively). Therefore, it might well be true that the species specific traits that determine competitive strength of adult plants are intensified by overall biomass effects. Still, the fact that “10 g” of *C. canescens* as competitor have a significantly higher effect than “10 g” of *C. arenaria* clearly shows that species specific allocation strategies are relatively more important in adult plants.

For seedlings or small plants, however, biomass effects have a significant effect on competitive interactions and hence differences in initial plant size might influence the outcome of a competition experiment. Similar results have been found by Grace (1985, 1988) and Newbery & Newman (1978), whereas other studies revealed no influence of initial plant size on competitive interactions (Wilson 1988, Gerry & Wilson 1995). In the present study initial size could have been important for *C. arenaria*, where targets have been planted with considerably lower biomass compared to both other species (see methods). However, a similar experiment that has been conducted before with equal initial biomass (*C. canescens*: 0.12 ± 0.00 ; *H. pilosella*: 0.22 ± 0.02 ; *C. arenaria*: 0.20 ± 0.01 , results in $g \pm SE$) resulted in the same competitive hierarchy between plant species, even despite of the disadvantage for *C. canescens* at the start.

The three species selected for this study were very different in growth not only aboveground but also, and probably more importantly, in root structure (see species description). As competition in resource poor habitats predominantly occurs belowground (Wilson & Tilman 1991, 1993, Belcher et al. 1995, Twolan-Strutt & Keddy 1996, Cahill 1999, Rebele 2000) the differing root growth of the study species might be an important factor. *C. canescens* with its fine but very dense and extended root system might be in favour of gathering limited soil resources compared to the other two species and this species specific effect might over-compensate any influence of biomass. Still, despite of its strong competitive superiority in the adult-plant competition experiment, *C. canescens* is dominant only in early successional stages on sand in the field. The reasons for this “contradiction” are twofold: First, *C. canescens* needs unstable sand or at least open sand patches for vigorous growth in the long run. In the subsequently denser vegetation cover of later successional stages young bunches of the species are rarely encountered because successful establishment fails, an effect that has not been integrated in the present study (Marshall 1965, 1967, Boorman 1982, Frey & Hensen 1995). Second, the competitive superiority of *C. canes-*

cens decreases with increasing nitrogen availability and hence increasing nutrient accumulation during ongoing succession (personal measurements, data not shown).

In the seedling competition experiment no clear superiority of one species could be detected but rather we found that interspecific competition was higher than intraspecific competition in most cases. This is not unusual and has been found for the majority of studies reviewed by Goldberg & Barton (1992).

Conclusions

The natural habitat of the three species studied is characterised by frequent small scale disturbances (e.g. by ants or rabbits), which results in continuously occurring open patches which have to be recolonized either through seedlings or clonal growth. The present results indicate that at least if species propagate by seeds, the time in favour of other competing seedlings seems to be a rather critical parameter for a successful establishment under such conditions, because in seedlings, age is typically directly correlated with biomass. Hence, an earlier colonisation means an advantage of biomass over other seedlings which, according to the present data, then results in a higher competitive effect on neighbouring individuals. However, shortly after this pioneer phase, the importance of plant biomass decreases relative to the effect of species identity in determining competitive strength of plant individuals. Thus, competitive interactions become increasingly intricate once plants are established which is possibly due to different biomass allocation strategies of the competitors.

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