

Competition and herbivory during salt marsh succession: the importance of forb growth strategy

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Summary

- 1 Despite much debate about their importance, only a few field studies have evaluated the intensity of competition and herbivory.
- 2 *Artemisia maritima*, *Atriplex portulacoides* and *Plantago maritima*, three plant species which are common in European temperate salt marshes, were transplanted into different successional stages (15, 30 and 45 years old) of a temperate salt marsh. Biomass of each transplant was measured as the response variable to treatments that manipulated competition and the level of herbivory.
- 3 All species were shown to be negatively influenced by both competition and herbivory, with competition being in general of greater importance than herbivory. No change could be detected during succession in the intensity of either competition or herbivory. Their combined impact, however, increased over succession for *Atriplex*, although no trend was observed for the other two species.
- 4 Both biomass and allocation patterns reflected further adaptations of these salt-tolerant species to environmental stress and biotic interactions present in the salt marsh. *Plantago*, which is the best adapted to salinity, was shown to be markedly affected by competition and herbivory. *Atriplex* showed less response to herbivory and little response to competition, to which it is well adapted. The grazing-deterring *Artemisia* was influenced by herbivory only as a seedling.

Key-words: *Artemisia maritima*, *Atriplex portulacoides*, competition, herbivory, *Plantago maritima*, productivity gradient, salt marsh, succession

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Introduction

Theoretical relationship between competition intensity and succession was proposed as early as 1916 (Clements 1916; Connell & Slatyer 1977), but its nature is still vigorously debated (Grime 1979; Tilman 1986, 1988; Glenn-Lewin & van der Maarel 1992). Of the two opposing views (Grace 1990), one (Grime 1973; Grime 1979) predicts that the intensity of competition will increase during succession because the abiotic disturbance that initiates succession will mean that early successional plants will never grow sufficiently close together to compete for resources. In contrast, Tilman (1985, 1988) predicted

that the intensity of competition will not change during succession, but there will be a shift from competition for below-ground resources early in succession to competition for light during later stages (Tilman 1988). Supporting this latter view, Oksanen (1990) argues that in early successional stages plants will be adapted to the level of disturbance, and competition for soil resources will thus be strong.

Herbivory is another possible factor in successional dynamics, but its role is poorly understood (Hixon & Brostoff 1996). In some studies, herbivory accelerates plant species replacement (Brown 1990), whereas in others it retards succession (Brown 1990; Davidson 1993). White (1984) argues that the strong influence on plant performance that herbivores are likely to exert in the stressful, early successional stages could be related to the accumulation of stress proteins, which in turn would make them attractive to nitrogen-limited herbivores. Oksanen *et al.* (1981) subscribe to the opposite view, claiming that plant biomass is initially too low to support an influential

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herbivore population, and predicting that herbivores will become more abundant as plant biomass increases during succession (unless carnivorous predators limit the population size of herbivores). However, the impact of a herbivore on a plant may depend on factors such as time of grazing and the plant's susceptibility to damage, as well as on the amount of biomass it removes (Edwards & Gillman 1987) and, possibly, to timing of grazing, vulnerability of the plant species, and so forth.

This study addresses the role of competition and herbivory during salt marsh succession on the island of Schiermonnikoog (Wadden Sea, The Netherlands). Three plant species were transplanted into different successional stages, corresponding to different levels of a productivity gradient, and both competition and herbivory were manipulated to test their variation during succession. Natural herbivores, which are abundant in the study system, include migratory birds as well as resident lagomorphs.

Methods

SITE DESCRIPTION

Sand accretion by the sea extends the Dutch barrier island of Schiermonnikoog ($53^{\circ}29' N$, $6^{\circ}18' E$) eastwards, and the bare initial stages of primary succession are continually being created. Clayey material is gradually deposited on top of the sand, providing an increasing amount of nutrients for the nitrogen-limited salt marsh system (Van Wijnen & Bakker 1997; Van Wijnen & Bakker 1999). Different successional stages are therefore found adjacent to each other, and represent a chronosequence (Pickett 1987; Olff *et al.* 1997) whose vegetation and succession is detailed in Olff *et al.* (1997).

Experimental sites represented three early stages of the succession (15, 30 and 40 years old), with increasing vegetation biomass and rates of nitrogen mineralization, and decreasing light availability (Table 1). The system has an elevation of *c.* 30 cm

above mean high water, is naturally grazed both by the resident brown hare *Lepus europaeus* and brent goose *Branta bernicla bernicla* during spring staging. On average, their combined grazing pressure is highest at successional stage 1, decreasing toward the later stages (Van de Koppel 1997; Table 1).

Three common salt marsh species, *Artemisia maritima*, *Atriplex portulacoides* and *Plantago maritima* (referred to hereafter by their generic names only; nomenclature follows Van der Meijden *et al.* 1990), were chosen to represent different levels of cover, palatability, growth form and life strategy (Table 2). *Artemisia* is a mid-successional matrix species (*sensu* Grubb 1986) that is dominant in terms of cover as well as biomass, as is *Atriplex*, which is a late successional species found in slightly lower elevation sites (about 20 cm above MHW, Van Wijnen *et al.* 1997). Neither *Atriplex* nor *Plantago* reach dominance at any of the successional stages monitored. All plants are perennials, but while the early successional *Plantago* is a rosette species and is therefore confined to open sites where much of the light reaches ground level, *Artemisia* and *Atriplex* are taller, shrubby plants. *Plantago* is a common food plant of the geese that forage on the salt marsh during spring staging (Prop & Deerenberg 1991). *Atriplex* and *Plantago*, and sometimes *Artemisia*, are all browsed by hares, the main herbivore of the system (Van der Wal *et al.* 2000c).

EXPERIMENTAL DESIGN

The design consisted of a full-factorial transplantation experiment. Treatments were arranged in blocks, each consisting of two levels of competition, two levels of herbivory, three species and two life stages of the plants, and therefore comprising 24 plots (each 30×30 cm). Two sets of five replicate blocks were established within each successional stage, with the sets separated by several hundred metres to allow full evaluation of the gradient in vegetation biomass. Biomass was determined for

Table 1 Site characteristics of the three successional stages. Numbers shown are mean \pm standard error; different letters indicate significant differences within rows (Tukey's Honest Significant Difference test)

Successional stage (age)	1 (15 years)	2 (30 years)	3 (40 years)
Dominant species	<i>Limonium vulgare</i> , <i>Puccinellia maritima</i> , <i>Festuca rubra</i>	<i>Artemisia maritima</i> , <i>Festuca rubra</i>	<i>Artemisia maritima</i> , <i>Festuca rubra</i> , <i>Limonium vulgare</i>
Above-ground biomass (g dry weight m ⁻²)	452 ± 53 a	627 ± 33 b	793 ± 59 b
% live biomass (g dry weight m ⁻²)	90 ± 2.4 a	76 ± 2.5 b	66 ± 2.8 c
Canopy height (cm)	11 ± 0.5 a	17 ± 1.2 b	20 ± 0.8 c
Light intensity at soil (% PAR)	98 ± 0.6 a	80 ± 3.0 b	74 ± 2.9 b
% bare soil	37 ± 2.7 a	0.6 ± 0.2 b	0.6 ± 0.3 b
N mineralization rate (g m ⁻² for top 10 cm)	3.8 ± 0.8 a	6.4 ± 0.5 b	8.9 ± 0.9 c
Grazing pressure (% living biomass removed)	7.9 ± 1.0 a	6.9 ± 0.8 a	5.7 ± 0.8 a
Elevation (min/max) (cm above MHW)	31.2 (24.7/35.7)	29.7 (26.0/34.5)	28.5 (24.4/35.4)

Table 2 Comparison of plant characteristics of the three target species

Species	Life strategy ¹	Main storage organ	Growth form	Average cover (% ± 1 SE) (n = 10 relevées per stage)		
				Stage 1	Stage 2	Stage 3
<i>Artemisia maritima</i>	SC	Tap root and stem base	Shrubby forb	4.8 (1.5)	43.0 (4.7)	36.0 (5.0)
<i>Atriplex portulacoides</i>	SC	Stem and shallow roots	Shrub	1.3 (0.2)	0.3 (0.2)	0.1 (0.1)
<i>Plantago maritima</i>	S	Tap root	Rosette forb	1.4 (0.2)	0.3 (0.2)	0.1 (0.1)

¹ S = stress adapted species, SC = stress adapted competitor, sensu Grime *et al.* (1988).

² According to Prop & Deerenberg (1991) and Van der Wal *et al.* (2000c), geese feed only on *Plantago*, hares make use of all plant species.

each site where the replicates were grouped. This resulted in 24 plots per block × 3 stages × 10 replicates = 720 plots.

To manipulate herbivory, the plots were fenced with chicken wire (4-cm mesh size, 50 cm high: the no grazing treatment, NG), or remained unfenced (the full grazing treatment, FG). FG and NG plots were kept some metres apart so that herbivores were not deterred from grazing the FG treatment by proximity of the cages.

Competition was achieved by transplanting target individuals into the vegetation naturally present at the experimental plots (the all neighbours treatment, AN), or (for the no-competition treatment, NN) to plots where all above-ground vegetation had been removed with electric hand shears. A buffer zone of 20 cm was left between the two competition treatments. The borders of the NN plots were trenched to a depth of about 30 cm with a knife, to sever rhizomes of adjacent plants, and green garden mesh with a hole in the centre to take the target individual was used to prevent drying out and soil rupture. Facilitative effects of the vegetation, which are thought to be due to the prevention of hypersalinity and soil drought (Bertness & Hacker 1994), may therefore have been less readily detected. The use of mesh may also have introduced some error into our assessment of the relative competition index (see below), but as our main focus was on resource competition we regarded this as a minor complication compared to the increased mortality if plants were unprotected. Re-growth of the cut vegetation was eliminated by manual weeding every other week for the whole experimental period.

Seedlings of *Artemisia* and *Plantago* were grown in a glasshouse from a mixture of seeds collected at all three successional stages. *Atriplex* seedlings and mature plants of all species were taken from the 30-year-old stage 2. Mature plants were removed in a piece of turf (about 20 cm diameter, 12 cm deep), leaving the root stock of *Artemisia* and the taproot of *Plantago* intact, while root connections within *Atriplex* stands were severed to produce individual transplants. Individuals were manually separated and washed free of adherent soil. Both seedlings and mature plants of the three test species were transplanted into a c. 10 cm deep slit in the soil of the prepared plots, which was then closed manually. Species and life stages were allocated at random to paired AN and NN competition plots, which were grouped into fenced and non-fenced areas.

The transplanting took place between 15 and 22 April 1997. Dead plants were replaced on 25 April and again around 11 May 1997. Survival of all plants, flowering and occurrence of insect bite marks were recorded at the end of April, at the beginning of May, June and July, and at the final harvest which was between 23 and 30 September 1997.

MEASURING PERFORMANCE

Plants were excavated, transported to the field station and stored at -12°C until further processing. Thawed plants were rinsed in water and separated into leaves, other above-ground parts and roots. Most fine roots were washed off, so only roots attached to the above-ground parts were included, resulting in a slight underestimation of below-ground weight. Plant parts were dried at 70°C to constant weight (approximately 48 h) and weighed to the nearest milligram.

CALCULATION OF INDICES

For the interpretation of competition and herbivory, indices were calculated according to Grace (1995), modified by Markham & Chanway (1996). Average values for the five blocks within each stage \times species \times treatment combination were used for calculation (groups where $n < 2$ were omitted). The relative competition index (RCI) is calculated from the difference between NN and AN divided by the biomass of the heavier of the two, X . This leads to an index between 1 and -1 (Markham & Chanway 1996). So as not to confound competition and herbivory, RCI-values were calculated only for ungrazed plots.

$$\text{RCI} = \frac{\text{biomass in NN NG}}{\text{biomass in AN NG}} - 1 \quad \text{eqn 1}$$

Positive values mean that the target plant suffered a reduction in biomass, while negative values indicate facilitating effects of the treatment. An RCI of 0.6, for instance, should be interpreted as a 60% reduction in biomass due to competition.

A separate, but analogous, relative herbivory index, RHI, was calculated for competition-free plots.

$$\text{RHI} = \frac{\text{biomass in NN NG}}{\text{biomass in NN FG}} - 1 \quad \text{eqn 2}$$

The relative competition-herbivory index RCHI, which serves as an indicator of the added effects of both competition and herbivory (Bonser & Reader 1995), is then defined as:

$$\text{RCHI} = \frac{\text{biomass in NN NG}}{\text{biomass in AN FG}} - 1 \quad \text{eqn 3}$$

STATISTICAL ANALYSIS

Log_{10} -transformed biomass data (Sokal & Rohlf 1995) were analysed, employing the Generalized Linear Model procedure of SAS (SAS Institute Inc.

1989). Transplant mortality resulted in an unbalanced data set. The ANOVA model was therefore simplified through stepwise removal of statistically unimportant interactions, with a removal threshold of $P = 0.1$ (Crawley 1993). Indices were analysed in the same way, using above-ground vegetation biomass as covariates; allocation patterns were analysed on the basis of leaf-weight ratios (LWR) and both indices and LWR were arcsine square-root transformed before analysis. All *post hoc* comparisons used Tukey's Honest Significant Difference test, correcting for multiple comparisons. Displayed values are means, error bars throughout the paper represent ± 1 standard error of the mean (SE).

Results

Of the factors investigated, competition generally had the strongest effect on plant biomass. Consistently for all three species, plants in NN plots were significantly heavier than in AN plots. Effects of successional stage were overruled by competition, so that the trend for biomass to increase with successional age was seen only in competition-free plots.

The effect of herbivory was only significant in half of the species-life stage combinations and less biomass was lost to grazers than to competition. Insect herbivory was rare and independent of treatment, it affected only one of the species (*Plantago*) and even here less than 5% of the individuals were attacked (data not shown). The interaction between competition and herbivory was, however, significant in mature *Atriplex* and in *Plantago* seedlings, indicating that protection from herbivores is important, with plants in NN plots more prone to grazing than those in vegetated plots (see below). The interaction between successional stage and herbivory was never significant, while the three-way interaction with competition was significant only once (Table 3).

For *Artemisia* and *Atriplex* biomass was greater when mature plants rather than seedlings were transplanted, while the opposite was true for *Plantago*, possibly due to transplantation shock in larger individuals. Treatment effects were generally similar for the two plant age classes.

Overall explained variance was generally high (67%; Table 3), with competition contributing an average of 29%. Although herbivory as main factor was sometimes significant, it explained less variance than competition, while 'block' and interactions generally added less than 10%.

ARTEMISIA MARITIMA

Competition reduced biomass significantly in all three stages (Fig. 1a). The mean weight of plants in AN plots was less than a third of that for plants in NN plots. The effects of competition were generally

Table 3 ANOVA results for the biomass of the three transplanted plant species: (a) mature plants, (b) seedlings. Data were log-transformed prior to analysis; *P*-values for significant effects are shown in bold; interactions not shown were omitted from the model (see Methods)

Source of variation	d.f.	<i>Artemisia maritima</i>				<i>Atriplex portulacoides</i>				<i>Plantago maritima</i>			
		MS	F	P	R ²	MS	F	P	R ²	MS	F	P	R ²
(a) Mature plants													
WITHIN + RESIDUAL (d.f.)	2	0.243	1.64	0.2052	0.027	0.159 (46)	0.98	0.3848	0.015	0.162 (35)	1.33	0.2766	0.024
STAGE	2	0.166	1.12	0.3601	0.243	0.245	1.53	0.1048	0.297	0.141	0.87	0.6362	0.185
BLOCK (STAGE)	26	4.761	32.17	0.0001	0.268	1.777	11.14	0.0017	0.083	5.893	36.35	0.0001	0.322
COMP	1	0.000	0.00	0.9641	0.000	1.404	8.81	0.0049	0.166	1.191	7.35	0.0103	0.065
HERB	1	1.031	6.97	0.0023	0.116	1.045	6.55	0.0033	0.097	0.454	2.80	0.0742	0.050
STAGE × COMP	2												
STAGE × HERB	2												
COMP × HERB	1												
STAGE × COMP × HERB	2												
Total explained variance					0.65					0.70			0.65
(b) Seedlings													
WITHIN + RESIDUAL (d.f.)	2	1.430	7.98	0.0013	0.063	0.259 (38)	0.66	0.5231	0.012	0.257 (25)	1.36	0.2742	0.020
STAGE	2	0.374	2.09	0.0196	0.206	0.339	1.31	0.2395	0.282	0.350	1.41	0.2051	0.214
BLOCK (STAGE)	26	19.654	109.71	0.0001	0.432	7.861	30.38	0.0001	0.273	11.942	46.49	0.0001	0.336
COMP	1	0.841	4.69	0.0366	0.018	0.205	0.79	0.3802	0.007	0.000	0.00	0.9857	0.000
HERB	1	0.359	2.01	0.1486	0.016								
STAGE × COMP	2	0.015	0.08	0.9202	0.000								
STAGE × HERB	2	0.432	2.41	0.1286	0.010								
COMP × HERB	1	0.621	3.46	0.0415	0.027								
STAGE × COMP × HERB	2												
Total explained variance					0.77					0.57			0.66

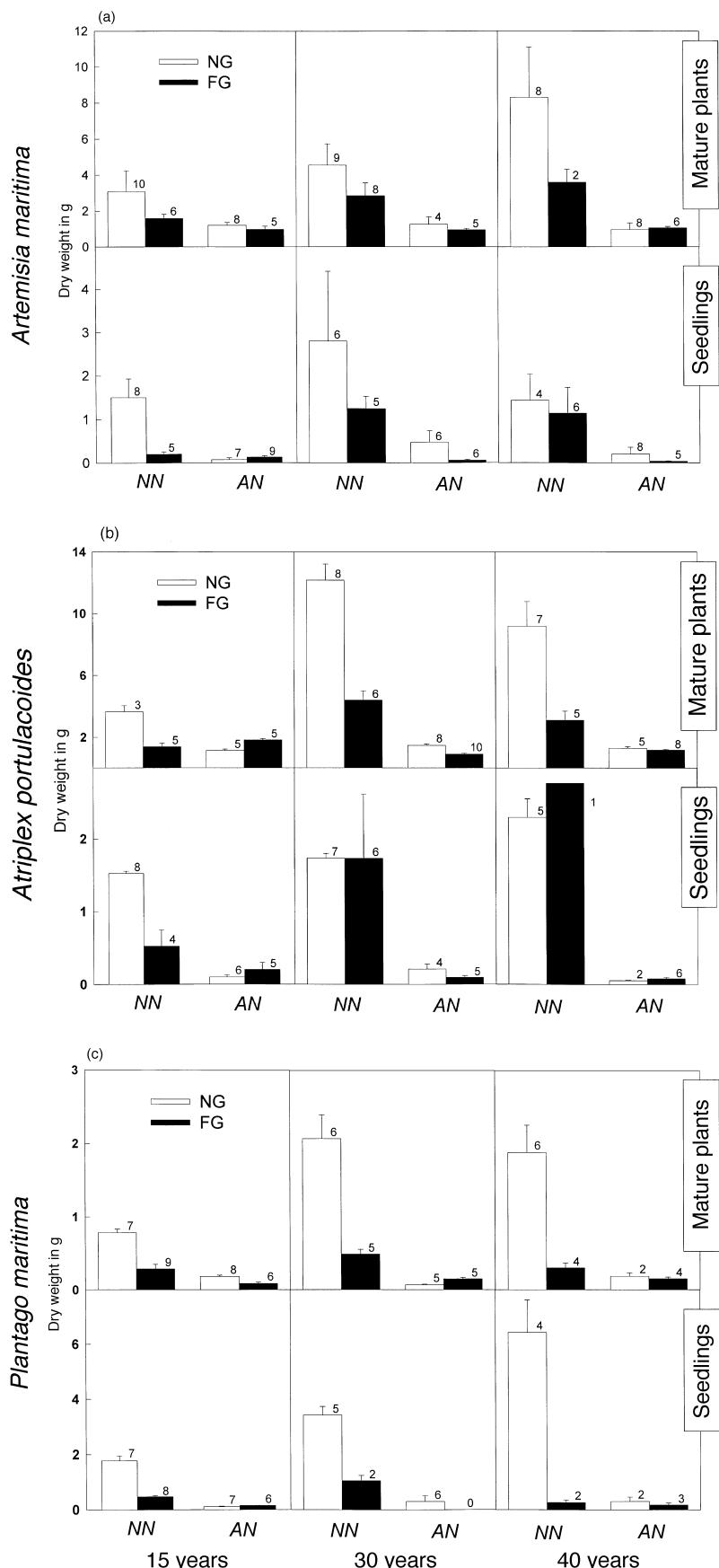


Fig. 1 Biomass of the three transplanted species at the three successional stages with and without competition (AN = all neighbours, and NN = no neighbours) and herbivory (NG = no grazing, and FG = full grazing). Note differences in vertical scaling. Error bars represent ± 1 standard error; numbers above bars refer to sample size, missing plants died during the experiment.

reduced when plants were grazed, and disappeared completely in successional stage 1.

The response to the different treatments was generally similar for seedlings and mature plants. In the first stage, however, both competition and herbivory had significant effects on the biomass of seedlings but only competition affected adult plants (Table 3).

Overall, an increase in biomass over the successional stages was apparent (Fig. 1a), although it was not significant. The differences between stages were, however, greater in mature plants when plants were released from competition (seen as the significant stage \times comp interaction; Table 3a).

In mature plants neither herbivory nor the interaction of herbivory and competition influenced significantly plant biomass (Table 3a), while herbivory had a negative impact on seedlings (Table 3b).

Atriplex portulacoides

All factors affected biomass, but competition was again most detrimental. In ungrazed plots in successional stages 2 and 3, competition lead to an 87% reduction in biomass and, although less pronounced, competition effects were still large (reductions of 73%) in the grazed plots.

Biomass did not differ significantly between successional stages despite an apparent positive trend for both seedlings and mature plants in ungrazed, competition-free plots (Fig. 1b).

Grazing had a significant effect only on mature plants (Table 3), which might be due to the small size of the seedlings making them unattractive to herbivores. Grazing reduced biomass by 30–50% in the competition-free plots (successional stage 1 and 2).

Plantago maritima

Competition was again the most important factor affecting biomass (Table 3), for both seedlings and mature plants (Fig. 1c). This lead to high seedling mortality in the AN plots (Fig. 1c), particularly in successional stages 2 and 3. As for the other two species, biomass was lowest at stage 1 (Fig. 1c).

Herbivores had a significant impact on mature *Plantago* in all stages (Table 3a). Effects were most pronounced in stage 3 and seedlings suffered more than mature plants, but only in competition-free plots (comp \times herb-interaction; Table 3b). This might be due to the fact that seedlings showed particularly vigorous growth when released from grazing and competition (Fig. 1c), while mature plants increased their biomass more moderately.

RELATIVE INTENSITY OF COMPETITION AND HERBIVORY DURING SUCCESSION

Overall, neither competition nor herbivory indices showed consistent trends in relation to vegetation biomass (Fig. 2) and neither species nor vegetation biomass proved to be significant in the ANCOVA ($P > 0.2$ for RCI and RHI).

Competition suppressed seedlings slightly more than mature plants (marginally higher RCI values in Fig. 2). Seedling performance in the AN plots relative to the NN ones was independent of the total biomass at that site, while mature plants seemingly suffered less at low vegetation biomass. Mature *Plantago* consistently showed higher RCI values than the other two species, but for seedlings no pattern can be recognized.

Reductions in biomass due to herbivory were less than those due to competition, and there were no consistent patterns at either life stage. In seedlings, RHI values even dipped below 0, indicating a benefit from allowing herbivory on the plots. There was no evidence of bite marks on the transplants in these cases (data not shown) and the benefit might be due to the grazing of neighbouring vegetation releasing seedlings from competition. When seedlings were grazed, biomass losses were more severe in low-biomass sites than in those with dense vegetation. Species differed in response, with RHI values tending to increase with above-ground biomass in mature *Artemisia* and *Plantago*, while values for mature *Atriplex* were scattered.

The combined effect of competition and herbivory, as displayed by the RCHI, was similar to that for competition alone, although it did tend to increase with increased vegetation biomass (Fig. 2). A significant trend could be detected for both mature plants (biomass: $F = 8.88$, $P = 0.031$, $r = 0.611$; species: $F = 5.50$, $P = 0.055$; interaction: $F = 6.10$, $P = 0.046$) and seedlings (biomass: $F = 9.09$, $P = 0.030$, $r = 0.611$; species: $F = 5.46$, $P = 0.055$; interaction: $F = 6.17$, $P = 0.043$). However, if the lowest biomass for *Atriplex* is excluded from the analysis, no significant trend in either mature plants or seedlings ($P > 0.1$) was found. *Artemisia*, being relatively little influenced by grazing, shows similar values for the RCI and RCHI, as did *Atriplex*. *Plantago*, however, has a very high RCHI value, indicating poorer performance in plots that were both grazed and vegetated. Many seedlings were killed in grazed AN plots, with those remaining being reduced in biomass by 90% or more.

RESOURCE ALLOCATION IN THE THREE SPECIES

Comparison of the three species (Fig. 3, where only the main factors – successional stage, competition and herbivory – are depicted) shows that under

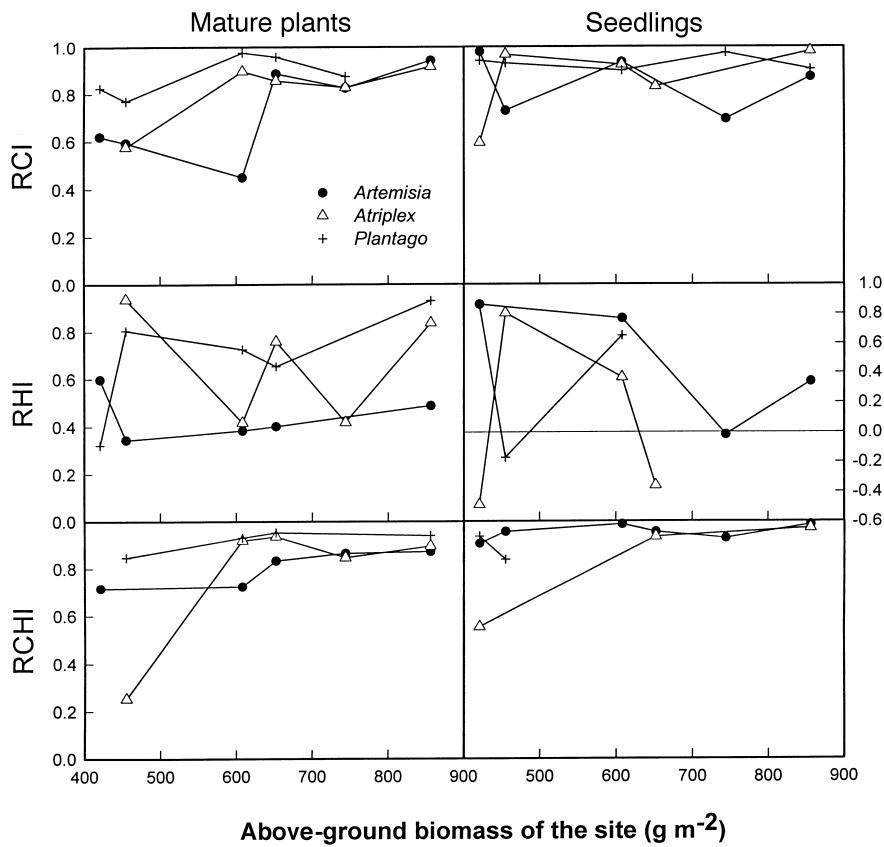


Fig. 2 Relative competition and herbivory indices along the successional gradient. Each of the three stages was represented by two substages (with differing biomass), each with five experimental blocks (see Methods). Data not shown if any treatment (or control) lost four of the five block values due to plant mortality. Note difference in index scale for RHI for seedlings.

'optimal' conditions, i.e. no grazing and no competition, the rosette plant *Plantago* has more biomass present in the leaves (*c.* 60%) than either *Artemisia* (*c.* 50%) or *Atriplex* (*c.* 30%). *Plantago* responded strongly to competition, reducing its allocation to leaves to only 12%, which can be explained by the observation that its leaves were thin and elongated, indicating shading by the surrounding vegetation. *Artemisia* and *Atriplex* showed similar patterns of response to the various treatments. Competition affected *Artemisia* more than *Atriplex*, reducing leaf biomass by more than 50%, compared to *c.* 30% for *Atriplex*. In grazed plots, *Artemisia* also showed a slightly stronger investment in storage and roots, while *Atriplex* hardly seemed to be affected.

All three species responded strongly to competition by allocating more biomass to roots and, where present, to stems; they generally had significantly less biomass as leaves. In the presence of competition, leaves comprise only 20% of the plants biomass and 50% of the biomass can be found in the stems of *Artemisia* and *Atriplex*. *Plantago*, being a rosette species, lacks a stem, but the below-ground parts serve for nutrient uptake as well as storage.

The response of seedlings is generally consistent with that of the mature plants of the same species. However, seedling leaf biomass is higher than in mature plants, possibly because they have not yet developed an extensive root and stem system.

Grazing caused a relative lowering of leaf biomass in all three species, probably reflecting off-take by herbivores. However, the proportion of biomass in leaves of grazed plants was still significantly higher than in plants suffering from competition (with the exceptions of mature *Artemisia* and *Atriplex* seedlings). The investment in leaves meant a reduction in the proportion of biomass allocated to the stem, except for mature *Atriplex* where no change in the proportion of stem biomass could be observed. The reduction of below-ground biomass due to grazing in *Plantago* is thus analogous to reduction in storage capacity, rather than a reduction in nutrient uptake capacity.

Discussion

The results clearly indicate the importance of competition and herbivory for the performance of salt

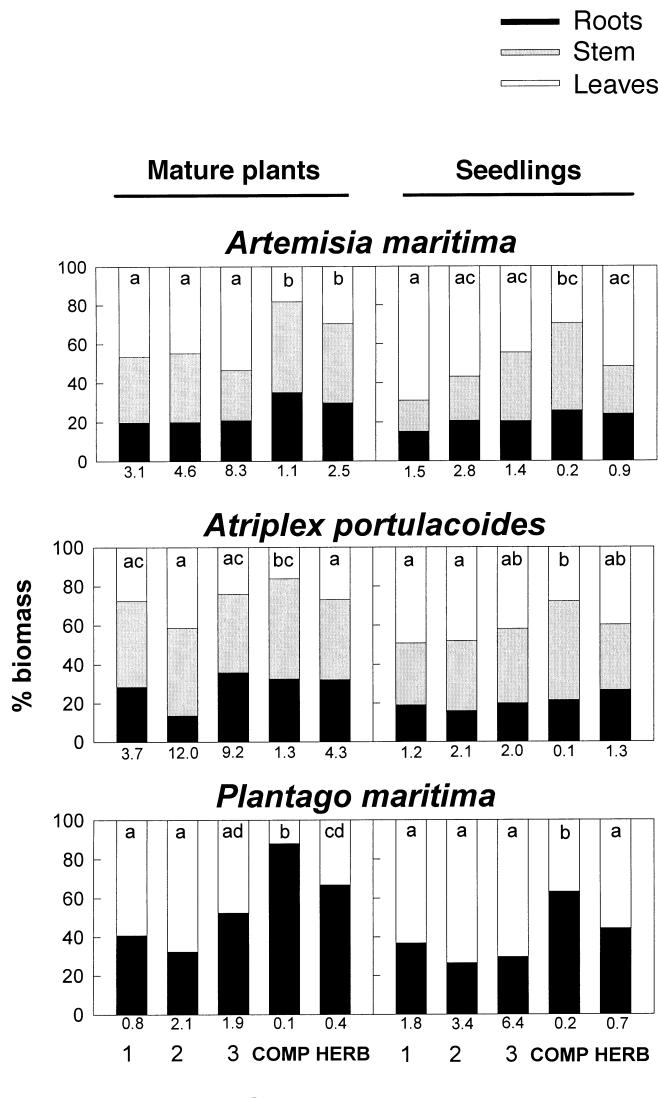


Fig. 3 Allocation patterns of the three transplanted species for mature plants (left hand side) and seedlings (right hand side). The percentage biomass found in roots and rhizomes and in leaves (and for *Artemisia* and *Atriplex* also in stems) is depicted for the three successional stages (1, 2 and 3) under 'optimal' conditions (i.e. NN and NG), for plants under competition (COMP; AN and NG) and for plants under grazing (HERB; NN and FG). For competition and herbivory, the stages were pooled together. Numbers under the bars are average biomass (g dry weight). Different letters indicate significant differences in leaf weight ratio ($P < 0.05$) according to Tukey's Honest Significant Difference post hoc comparison.

marsh species. In almost all cases competition had a higher impact than herbivory, although species differed considerably in their response to the treatments. Although the absolute grazing intensity on the vegetation is known to decrease from successional stages 1–3 (Table 1), the same trend was not observed for the transplanted specimens. *Plantago* was most susceptible to both competition and herbivory treatments, followed by *Artemisia* and then *Atriplex*, neither of which both showed a marked response to herbivory. There was a trend toward an increase in biomass with increasing successional stage in NN NG plots, which can be explained by the higher nitrogen availability in the older success-

sional stages (Olff *et al.* 1997; Van Wijnen & Bakker 1999).

THE INTENSITY OF COMPETITION AND HERBIVORY

Theories differ in their predictions about the importance of herbivory along successional or productivity gradients. Oksanen *et al.* (1981) suggested that herbivory would increase along with system productivity. If, however, herbivores are able to move freely along a spatial productivity gradient, herbivory will be more important at the unproductive end of the gradient (Bonser & Reader 1995; Van de

Koppel 1997). While Edwards & Gillman (1987) describe herbivory as a marginal factor in early successional stages, Reader (1992) in a field experiment found that a large part of the mortality of plants in early successional stages was due to herbivory.

Neither the relative intensity of competition nor that of herbivory varied consistently (or significantly) along our productivity gradient. The impact of competition and herbivory acting in concert did, however, lead to a significant increase in the relative competition–herbivory index but only for one species (*Atriplex*). Light levels at the soil were very high in the early successional stages (Table 1) and the intensity of competition remained unchanged over the productivity gradient. It therefore seems probable that the nature of competition changed from competition for nutrients in the early successional stages to competition for light in the later stages. When the mechanisms of competition were analysed for *Triglochin maritima*, this shift was documented convincingly (Van der Wal *et al.* 2000a).

Our findings are in accordance with those of Wilson & Tilman (1991) who reported that there was no trend in RCI over a biomass gradient in an old-field experiment, and that any tendency was for lower competition intensity at higher productivity levels. Van der Wal *et al.* (2000a), working on the same salt marsh system as used in the experiment presented here, and A. van der Veen, C. Kaldewey & J.P. Bakker (unpublished data) studying dune succession, also found little variation in RCI values.

These results contrast with a general finding that studies addressing the question of the intensity of competition have typically shown that the net competition effects are smaller on less productive sites, and that effects there may even be facilitative (Goldberg 1990). This notion is supported by old-field experiments (Goldberg 1987) and by those of Bonser & Reader (1995) who report a steep increase in the value of RCI with increasing productivity, levelling off at about 350 g m^{-2} above-ground biomass. When making an intercontinental comparison, however, Reader *et al.* (1994) found that *Poa pratensis* did not experience higher competition intensity at higher biomass, except for at a site at Groningen where the biomass range was by far the greatest. It therefore seems that an increase in competition intensity with increasing vegetation biomass may be confined to systems where biomass of all sites studied remains low (Belcher *et al.* 1995).

Both theories (White 1984; Coley *et al.* 1985) and models (Oksanen *et al.* 1981; Huisman & Olff 1998; Huisman *et al.* 1999) predict that herbivory intensity will increase with biomass although, except for Bonser & Reader (1995), little supporting evidence is available. Our results, which show no increase in herbivore intensity with increasing vegetation biomass, do not conform with these expectations.

The three species studied do not appear to adjust the proportion of above-ground biomass to the different conditions of the three stages in a consistent manner. According to Tilman (1988), we would have expected a higher allocation to stem and leaves as a consequence of increasing competition for light in later successional stages. Despite the trend for lower allocation to roots in heavier individuals ($P < 0.02$ for mature *Artemisia*, mature and juvenile *Plantago* and *Atriplex* seedlings, not significant for mature *Atriplex* and *Artemisia* seedlings; NN NG plots) and an increase in individual biomass with age of succession, no trend is apparent for the root: shoot ratio over the three successional stages (Fig. 3).

DIFFERENCES IN FORB GROWTH STRATEGIES

The three plant species selected for the experiment differ greatly in their growth strategies. All plants growing in a salt marsh have to face the constraints imposed upon it by regular tidal flooding, and must therefore be ‘stress-adapted’ (Jefferies *et al.* 1979; Grime *et al.* 1988). It seems, however, that different additional strategies have developed in the three species: *Plantago* seems specialized in tolerating hypersaline conditions, *Artemisia* copes better with herbivory, while *Atriplex* seems adapted to competition.

Plantago is able to grow over a broad range of elevations and soil nutrient levels (Jefferies *et al.* 1979; Olff *et al.* 1997), while coping with hypersaline conditions (Jefferies 1977), but it appears to be sensitive to both herbivory and competition (Fig. 2c). As with most plants facing abiotic stress, *Plantago* show an accumulation of stress compounds in its leaves, for example proline and betaine (Crawford 1989), and is thus attractive to herbivores (White 1984). Although competition is a significant factor throughout the analysis of transplant biomass (Table 3), it is most clearly the main factor in the case of *Plantago*, where the R^2 value of mature plants is the highest of all species.

If we consider the RHI values (Fig. 2), plant responses to herbivory are ranked as *Plantago* > *Atriplex* > *Artemisia*. Therefore, relative to the other species, *Artemisia* appears to be adapted to herbivory and is successfully defended by high amounts of secondary metabolic products, which give the plant its characteristic smell (Eissa *et al.* 1996; Narjissee *et al.* 1997). Although *Artemisia* seedlings were consumed by herbivores, the R^2 for their effect was low (< 2%; Table 3b). Geese avoid this plant species and hares restrict their consumption to seedlings and the basal stem of mature plants in winter (Van der Wal *et al.* 2000c) where the concentration of defence products is noticeably lower than

in the upper stem and leaves (C.F. Dormann & R. Van der Wal, personal observation).

Atriplex, as the tallest of the three plant species, might be expected to be competitively superior (Gaudet & Keddy 1988) and it does, in fact, dominate the lower salt marsh at this site (Huisman *et al.* 1993; Olff *et al.* 1997). As Fig. 3 shows, *Atriplex* reacted to competition with an increased allocation of biomass to stems, enabling it to overgrow and shade its neighbours. The impact of competition was therefore lowest for *Atriplex* (Table 3). Its potential to cope with anoxia and salt is limited by its nitrogen supply (Pigott 1969), and environmental stress therefore seems to be the major factor excluding it from the nutrient-poor, early successional stages, although hare-grazing also seems important for those seedlings that do establish (Van der Wal *et al.* 2000c). *Atriplex* outcompetes *Elymus athericus* (Bockelmann & Neuhaus 1999) despite its lesser stature, suggesting that it may be a vigorous competitor for below-ground resources. High competitive vigour in *Atriplex* might occur at the cost of vulnerability to mechanical damage, which can be due to ice-scouring as well as grazing. As a result, trampling and grazing by livestock excludes this plant species from most of the salt marshes in Europe, restricting its occurrence to creek banks (Jensen 1985; Scherfose 1993; Kiehl *et al.* 1996; Bakker *et al.* 1997).

CONSEQUENCES FOR SALT MARSH SUCCESSION

Over time, the early successional *Plantago* is replaced by the mid-successional *Artemisia*, which eventually will be replaced by the late-successional *Atriplex* (Olff *et al.* 1997; Drent & Van der Wal 1999). This successional replacement seems to be driven to a large extent by the accumulation of nutrients. The vegetation changes from an open system with a low canopy to a dense stand dominated by tall plants (Van Wijnen *et al.* 1997).

Differences among target species in their response to competition and herbivory are consistent with the sequence of their replacement. Of the three species, *Plantago* is most susceptible to competition for light, due to its prostrate growth form. As was found for *Triglochin maritima* in the same salt marsh system (Van der Wal *et al.* 2000a), this plant species is likely to be outshaded as the productivity of the marsh increases and taller plants like *Artemisia* and *Atriplex* are able to grow. *Atriplex* responded to competition with an increase in allocation to stem tissue, which allows this plant species to overtop mid-successional species such as *Artemisia*.

Herbivory had the greatest impact on *Plantago*. According to the theories of White (1984) and Coley

(1987), early successional species such as *Plantago* are more palatable than late successional species such as *Atriplex* or *Elymus athericus*. These authors argue that the impact of disturbance is higher in the early stages, and plants thus contain higher concentrations of stress proteins, which makes them attractive to herbivores (Reader & Southwood 1981; White 1984; Davidson 1993). Salt marsh plants of early stages and low elevation, such as *Plantago maritima*, *Puccinellia maritima* and *Triglochin maritima* are indeed the preferred food species of the highly selective brent geese (Prop & Deerenberg 1991). The combination of herbivory and competition is likely to restrict the occurrence of *Plantago* to younger parts of the salt marsh. Losses due to herbivory in *Artemisia* seem to be low and restricted to seedlings. With an increase in available nutrients during succession, *Artemisia* takes over but is eventually outcompeted by *Atriplex*. Although herbivory during the growing season was found to be unimportant, winter grazing by hares has been shown to delay the stage at which *Atriplex* becomes dominant by more than 25 years (Van der Wal *et al.* 2000c).

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