

The Impact of Herbivory and Competition on Flowering and Survival during Saltmarsh Succession

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Abstract: For succession, the establishment and turnover of plants, in terms of generative spreading and renewal, is of crucial importance. Especially the success of seedling establishment into the existing vegetation might be of prime importance for the further development of plant species composition. Flowering, on the other hand, is the necessary first step towards generative output and later seed set. In a chronosequential gradient of a saltmarsh succession, we investigated the performance of transplants of three common species under different conditions: *Artemisia maritima*, *Atriplex portulacoides* and *Plantago maritima* were transplanted as seedlings and mature plants into plots in early-, mid-, and late-successional stages (15, 30 and 40 years) on the Dutch island of Schiermonnikoog. Natural herbivory (by hares and geese) and neighbourhood competition were excluded in a factorial design. Flowering and survival rates of the three species were generally greatly reduced under natural conditions, compared to competition- and herbivory-free plots. The survival rates of *Artemisia maritima* and *Plantago maritima* reflect their position as early-successional species: early in succession, both show their highest survival and abundance. For late-dominant *Atriplex portulacoides* a different explanation has to be invoked for the medium-high survival and low abundance: probably winter grazing by hares and the importance of a high nitrogen supply rate, rather than flowering and survival, determine its low abundance in the early and mid-phase of this saltmarsh succession. Some long-term impacts of herbivores affecting flowering and survival are discussed.

Key words: *Artemisia maritima*, *Atriplex portulacoides*, *Plantago maritima*, saltmarsh, Schiermonnikoog, succession.

Introduction

Succession is one of the main framework concepts in plant ecology (Connell and Slayter, 1977^[10]; Glenn-Lewin and Van der Maarel, 1992^[21]). Different theories have been formulated to describe (Noble and Slayter, 1980^[33]), analyse (Pickett et al., 1987^[36]) and predict (Grime, 1979^[22]; Tilman, 1986^[42]) successional plant species replacement. The majority of studies in the literature are based on secondary successions (Connell and

Slayter, 1977^[10]; Glenn-Lewin and Van der Maarel, 1992^[21]), while primary succession series provide famous and exotic exceptions (Glacier Bay: Cowles, 1899^[13]; Lake Michigan Dunes: Cooper, 1923^[11], 1939^[12]). Accordingly, little is known about the mechanisms behind plant species replacement pattern in these primary successions. Although the impact of competition has been studied in detail in old-field successions (Tilman, 1987^[43]; Tilman and Wedin, 1991^[45]), only speculation concerning this agent, other than herbivory, have been advanced for the temporal species pattern on newly-formed ground (Connell and Slayter, 1977^[10]; Grime, 1979^[22]; Tilman, 1988^[44]; Davidson, 1993^[14]).

In the present study, we report from a competition and herbivory experiment performed in a primary saltmarsh succession (Roosen and Westhoff, 1985^[40]; Leendertse and Rozema, 1997^[29]; Olff et al., 1997^[34]). Saltmarshes are ideal for the examination of structuring factors: the vegetation harbours few plant species and human impact on the system is low, especially on Barrier island saltmarshes. Different studies have emphasized the importance of competition, as well as facilitation in this system (Vince and Snow, 1984^[56]; Bertness and Ellison, 1987^[5]; Ellison, 1987^[18]; Bertness, 1991^[4]; Pennings and Callaway, 1992^[35]; Bertness and Shumway, 1993^[8]), and evidence of impacts of grazing by natural herbivores such as hares and geese is increasing (Mulder and Ruess, 1998^[31]; Drent and Van der Wal, 1999^[16]; Van der Wal et al., 1999^[49]).

In the reproductive cycle of plant species (Fig. 1) some phases are more susceptible to competition and herbivory than others. Flowering, for example, can serve as an indicator of all environmental conditions adverse to the plants reproductive performance. Seed abortion and the decay of seeds in the soil are under abiotic rather than biotic control (Silvertown and Lovett Doust, 1994^[41]) and thus of less interest in this context. There are no reports on seed predation of seedbanks from saltmarshes, although a removal (as well as import) of seeds by tidal waters is possible (Huiskes et al., 1995^[24]). The establishment of germinated seeds, however, is dependent on environmental conditions and biotic interactions: light competition and high grazing pressure due to higher palatability of seedlings (White, 1984^[57]; Hartley and Jones, 1997^[23]) may cause high mortality and thereby potentially lead to differential performance of plant species during succession. Here, we present results of the flowering and survival rates of three saltmarsh plant species, *Plantago maritima*, *Artemisia maritima* and *Atri-*

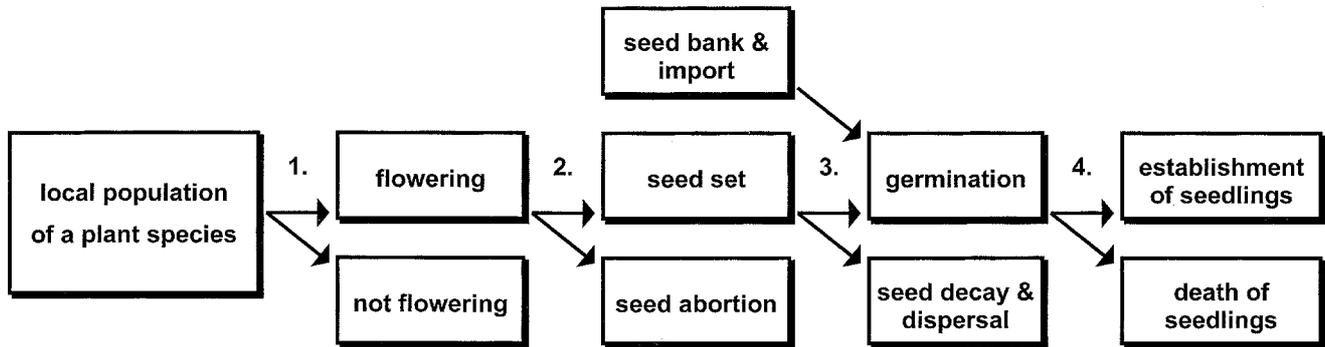


Fig. 1 The main phases of generative reproduction. Steps 2 and 3 are assumed not to be under the influence of competition and/or herbivory.

plex portulacoides, characteristic for early-, mid- and late-successional stages, respectively. We focus on the impact of biotic interactions, and their consequences for saltmarsh succession.

Materials and Methods

Site description

The study was performed on the Dutch sandy barrier island of Schiermonnikoog (53°29'N, 6°18'E). Sand accretion by the sea extends the island eastwards, continually creating bare initial states of primary succession. With time, clayey material is deposited on top of the sand, providing an increasing amount of nutrients for this nitrogen-limited system (Kiehl et al., 1997^[28]; Van Wijnen and Bakker, 1997^[52]; Van Wijnen and Bakker, 1999^[53]). Different successional ages are thereby found beside each other, representing a chronosequential gradient from commencement to 100 years of succession (Pickett, 1987^[36]; Olff et al., 1997^[34]). Detailed accounts on vegetation and succession on this saltmarsh are given in Olff et al. (1997^[34]).

Three stages, including 15 years (early-successional), 30 years (mid-successional) and 40 years (late-successional), were chosen as experimental sites. Along these sites, species composition changes, vegetation biomass, height and nitrogen mineralization rate increase, while the number of plant species, the amount of bare soil and light availability in the vegetation decrease (Table 1). At this elevation (Table 1), the system is naturally grazed by European hare *Lepus europaeus* and spring staging Barnacle goose (*Branta leucopsis*) and Brent goose (*Branta bernicla bernicla*). Their grazing pressure is highest at stage 1, decreasing toward the later stages (Van de Koppel et al., 1996^[47]).

Three plant species have been chosen for the experiment: *Artemisia maritima* L., *Atriplex portulacoides* L. and *Plantago maritima* L. (referred to hereafter with their genus name only; nomenclature follows Van der Meijden et al., 1990^[48]). They were chosen as common saltmarsh plants, representative for different stages of saltmarsh succession. *Artemisia* is a matrix species (dominant in cover as well as biomass), as can be *Atriplex* in slightly lower sites (about +20 cm MHT, Van Wijnen et al., 1997^[54]). All plants are long-lived, but while *Plantago* is a rosette species (therefore confined to open habitats where much of the light reaches ground level), *Artemisia* and *Atriplex* are

Table 1 Site characteristics of the three successional stages. Numbers in brackets refer to standard error, different letters indicate differences within rows (Tukey's honest significant difference test)

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>
Aboveground biomass ¹	452 ± 53 a	627 ± 33 b	793 ± 59 b
% live biomass ¹	90 ± 2.4 a	76 ± 2.5 b	66 ± 2.8 c
Canopy height ²	11 ± 0.5 a	17 ± 1.2 b	20 ± 0.8 c
Light intensity at soil ³	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 ⁴	3.8 ± 0.8 a	6.4 ± 0.5 b	8.9 ± 0.9 c
Grazing pressure ⁵	7.9 ± 1.0 a	6.9 ± 0.8 a	5.7 ± 0.8 a
Elevation ⁶ (min/max)	31.2 (24.7/35.7)	29.7 (26.0/34.5)	28.5 (24.4/35.4)

¹ sampled on 12 plots per stage per m²;
² measured with styrofoam disc (Ø 30 cm, 60 g) falling on calibrated cane; 10 plots per stage, with 5 averaged subsamples per 4 m² plot;
³ in %, derived from 50 measurements of photosynthetic active radiation in 10 plots per stage;
⁴ in g·m⁻² for the top 50 cm of the soil, calculated with biomass data following Van Wijnen et al. (1999^[53]);
⁵ food off-take in % living aboveground biomass removed, calculated with the given biomass data, dropping counts in ten 4 m² plots per stage (data not shown), digestibility data of vegetation for hares and geese, corrected for non-organic content of droppings (Van de Koppel, 1997^[46]);
⁶ measured in the middle of each NG and FG block (N = 20 per stage) as cm above mean high water.

shrubby, taller-growing plants. *Plantago* is a common food plant of the geese that forage on the saltmarsh during spring staging (Prop and Deerenberg, 1991^[39]). *Atriplex* and *Plantago*, and sometimes *Artemisia* as well, are all browsed by hares (Drent and Van der Wal, 1999^[16]).

Experimental design

The experimental design consisted of a full-factorial manipulation of herbivory and competition, with 10 replicates at each of three different successional stages. Both seedlings and ma-

Table 2 Results of logistic regression analysis of flowering events. All factors listed were incorporated in the final model. $-2 \cdot L$ refers to the log-likelihood ratio of a factor (or the model), df to the degrees of freedom for the respective factor (or model), p indicates the significance of a factor after removal from the final model, and R^2 represents the effect size of the factor (model)

Mature plants	$-2 \cdot L$	df	p	R^2	Seedlings	$-2 \cdot L$	df	p	R^2
<i>Plantago</i>					<i>Plantago</i>				
comp	24.82	1	0.0000	62.2	comp	12.80	1	0.0003	23.7
comp \times herb	9.92	1	0.0016	24.9	herb	4.05	1	0.0443	7.5
model	39.88	2	0.0000	87.1	model	54.22	2	0.0005	31.2
<i>Artemisia</i>					<i>Artemisia</i>				
herb	8.66	1	0.0033	10.8	comp	7.39	1	0.0066	23.0
stage	19.17	2	0.0001	23.8	herb	5.62	1	0.0177	14.0
comp \times herb	5.02	1	0.0251	6.2	stage	4.96	2	0.0838	17.5
comp \times stage	5.49	2	0.0643	6.8	model	32.13	4	0.0061	54.5
herb \times stage	8.46	2	0.0145	10.5					
comp \times herb \times stage	8.94	2	0.0115	11.1					
model	80.56	10	0.0010	69.2					
<i>Atriplex</i>					<i>Atriplex</i>				
comp	5.97	1	0.0145	7.4	comp	16.10	1	0.0001	49.5
herb	6.42	1	0.0113	7.9	herb	4.55	1	0.0329	14.0
comp \times herb	4.66	1	0.0309	5.7	stage	5.63	2	0.0598	17.3
comp \times herb \times stage	4.69	2	0.0961	5.8	model	32.53	4	0.0000	80.8
model	81.16	5	0.0700	26.8					

ture plants of the three test species were transplanted into the prepared plots as target individuals.

The seedlings of *Artemisia* and *Plantago* were raised from seeds in the greenhouse, while the *Atriplex* seedlings and all mature plants were taken from stage 2. For transplanting, a piece of turf with the respective specimen was cut out of the soil (about 20 cm \varnothing , 12 cm deep) and the individual plants were washed out and separated manually, thus being transplanted without adherent soil. This might have caused damage to the roots, probably resulting in a slightly higher mortality in all treatments following transplantation. The transplantation took place between 15 and 22 April 1997. As many seedlings, especially of *Artemisia*, died immediately after the transfer, all dead seedlings were replaced two and four weeks after initial transplantation. The main phase of the experiment began in early June 1996.

Competition was attained by transplanting the target individuals into the vegetation present at the experimental plots (all neighbours, AN), while for the no competition treatment all aboveground vegetation was removed with electric hand shears (no neighbours, NN). The borders of all plots (size 30 \times 30 cm²) were trenched to a depth of about 30 cm with a knife, to sever rhizomes of adjacent plants. Roots were not removed to avoid disturbance to the soil, and left to decay (Aarssen and Epp, 1990^[11]). To reduce loss of soil water content through evaporation and subsequent increase in salinity (Bertness et al., 1992^[6]), green garden mesh was fixed on the cleared plot, leaving a hole in the centre in which to place the target individual. Re-growth of the cut vegetation was eliminated by manually weeding every other week for the entire experimental period. To manipulate herbivory, the plots were fenced with chicken wire (4 cm mesh size, 50 cm high), or remained un-

fenced. The six different mature and juvenile specimens were randomly grouped next to each other in a sub-block. Two adjacent sub-blocks (AN and NN) were combined to be fenced (no grazing = NG) or not (full grazing = FG). In total, 10 replicates of the 4 treatments at three sites resulted in 120 plots per plant species and age, thus 720 experimental plots were established in the succession series.

From 4 June to 3 October 1996 survival and flowering status of all plants were recorded as simple binary data. As the plants were harvested by early October, no further observations on seed set could be done. The biomass results will be presented elsewhere (Dormann et al. submitted^[15]).

Statistical analysis

Data were analyzed by stepwise backward logistic regression using the log-likelihood ratio test criterion (Menard, 1995^[30]). Effect sizes (R^2 , in %) were calculated by dividing the log-likelihood value, multiplied by -2 , by the $-2 \cdot L$ value of the null model (Menard, 1995^[30]). The $-2 \cdot L$ value is analogous to the sum of squares in analysis of variance (ANOVA).

Results

Flowering

The flowering performance of early successional *Plantago* was significantly determined by competition and herbivory (Table 2). No flowering occurred in AN FG plots, i.e., under natural conditions, for either mature or juvenile plants (Fig. 2). Mature plants were in fact only flowering in NN plots, with a strong decrease in flowering percentage under herbivory (NN FG; Fig. 2). Treatments explained most of the variation in flow-

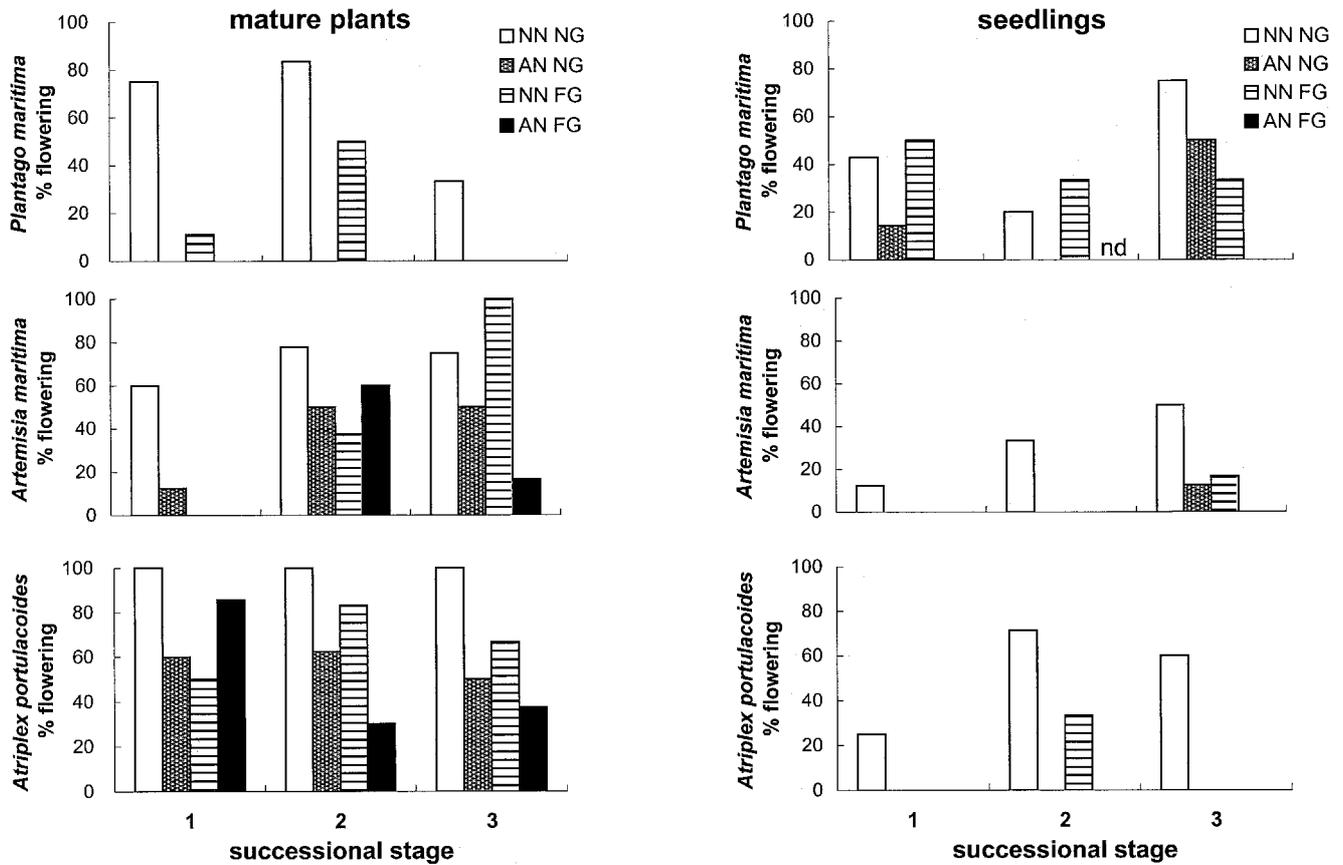


Fig. 2 Flowering percentages of mature plants and seedlings of the three species at the three successional stages. AN, NN, FG and NG refer to all neighbours, no neighbours, full grazing, and no grazing, respectively. The left bar at each stage represents the “optimal”,

and the right bar the “natural” conditions. “nd” indicates that all plants in this treatment had died, and thus no information on flowering percentage was available.

ering data of mature *Plantago* (87%), while only 31% of the variation for the juvenile plants could be explained (Table 2).

Mid-successional *Artemisia* showed no consistent response to treatments at the three stages, as far as mature plants are concerned (Fig. 2). Competition and/or herbivory almost completely prevented flowering at stage 1, always leaving some plants to flower in the two later stages (Fig. 2). This trend is significant (interactions of competition and herbivory with stage; Table 2), and the three factors explain as much as 69% of the occurring variation in the flowering of mature plants. In seedlings, any exposure to competition or herbivory drastically reduced flowering (Fig. 2). Only at stage 3 could juvenile *Artemisia* reach the state of flowering with competition or herbivory imposed, but failed to do so in AN FG plots. The model explained 55% of the variation, with competition being most important (Table 2).

Of the three species, mature plants of the late-successional *Atriplex* showed the least reduction of flowering under treatment conditions (Fig. 2). Effects of competition, herbivory and stage significantly contributed to the variation among plots (Table 2) and caused less flowering in all AN plots, especially the grazed ones (Fig. 2). However, differences among treatments were not as pronounced as in the other two species, and the model explained a modest 27% of the variation

(Table 2). For seedlings, the picture resembles that of mature *Plantago*: no flowering occurred in AN plots, with herbivory additionally preventing flowering in the NN plots of stage 1 and 3 (Fig. 2). Apparently stage 2 is slightly less adverse to *Atriplex* seedlings than the other two stages (almost significant effect of stage; Table 2). Competition, herbivory and stage as main factors explained 81% of the variation in the flowering data of *Atriplex* seedlings (Table 2).

Survival

The survival of mature plants determines the size of the local population of a plant species (Fig. 1). Perennial species possess reserves that are stored in tap roots (*Plantago*), stem base and upper rhizome (*Artemisia*) or in the stem and branches (*Atriplex*), and which allow them to survive periods of adverse environmental conditions, such as flooding, drought, hypersalinity, or winter. Accordingly, survival was shown to be less responsive than flowering in terms of % variance explained (Tables 2 and 3), and the absolute differences between control and treatments were lower (Figs. 2 and 3). On average, 19% of the variance in survival data could be explained by the manipulations (58% for flowering). Survival of seedlings of the three tested plant species showed a high stochastic proportion as well: here, only 16% of the variation could be attributed to treatment conditions (Table 3).

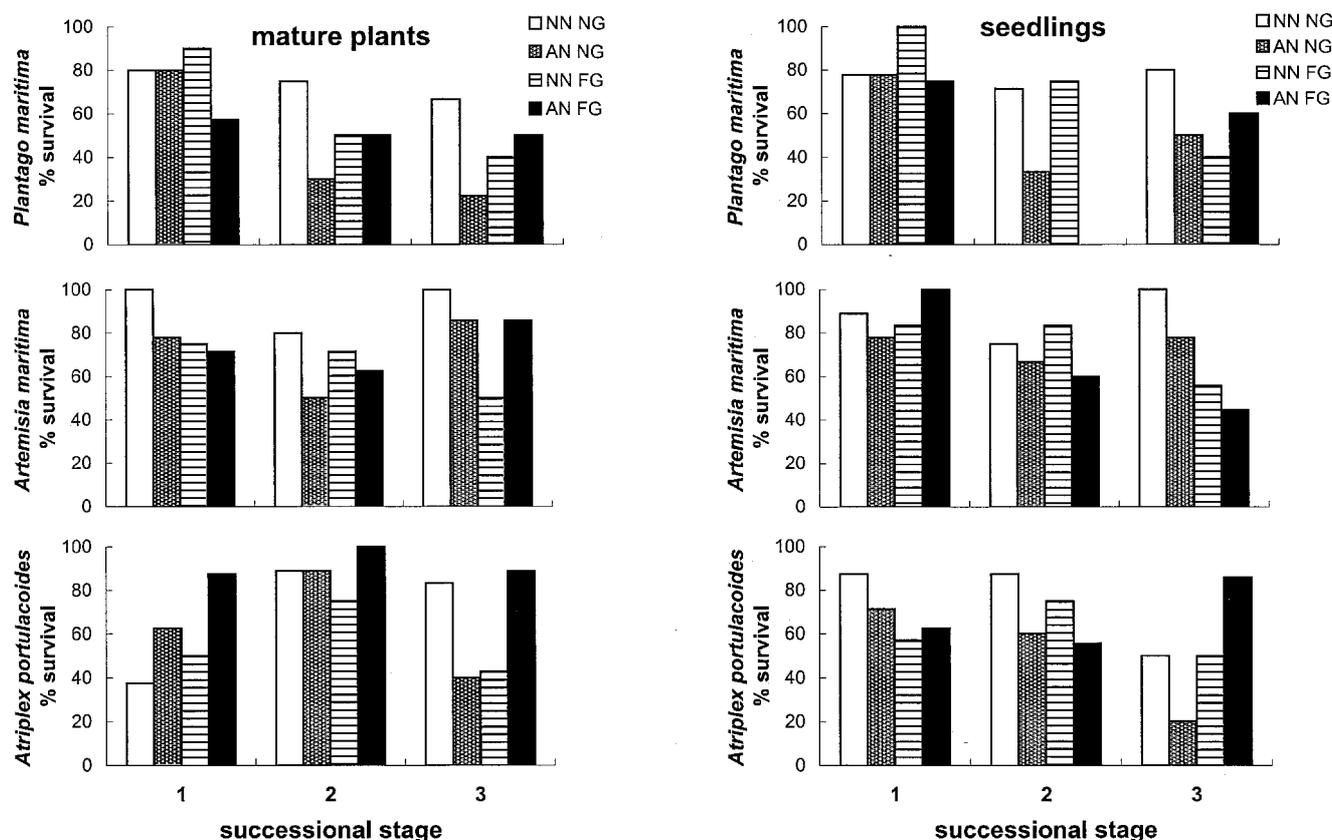


Fig. 3 Survival percentages of mature plants and seedlings of the three species. See Fig. 2 for abbreviations.

Table 3 Results of the logistic regression analysis of survival data. See Table 2 for abbreviations

Mature plants	-2 · L	df	p	R ²	Seedlings	-2 · L	df	p	R ²
<i>Plantago</i>					<i>Plantago</i>				
comp	4.41	1	0.0357	4.3	comp	5.84	1	0.0157	7.0
comp × stage	8.12	2	0.0172	7.8	herb × stage	6.73	2	0.0346	8.1
herb × stage	5.43	2	0.0663	5.2	comp × herb × stage	6.68	2	0.0355	8.1
comp × herb × stage	7.86	2	0.0196	7.6	model	82.99	5	0.0010	23.2
model	103.72	7	0.0088	24.9	<i>Artemisia</i>				
<i>Artemisia</i>					<i>Artemisia</i>				
comp	5.11	1	0.0239	5.9	comp × herb × stage	101.05	2	0.0080	9.6
herb	5.36	1	0.0206	6.2	model				
comp × herb	3.77	1	0.0521	4.4	<i>Atriplex</i>				
model	86.50	3	0.0079	16.5	<i>Atriplex</i>				
<i>Atriplex</i>					<i>Atriplex</i>				
stage	10.26	2	0.0059	11.0	stage	9.06	2	0.0108	9.0
comp × herb	10.49	1	0.0012	11.3	comp × herb × stage	7.07	2	0.0292	7.0
model	93.04	3	0.0020	22.3	model	100.86	4	0.0304	16.0

Survival of mature *Plantago* was significantly affected by competition and by interactions of competition, herbivory and stage (Table 3). At stage 1, differences between treatments were marginal, only the AN FG plots showed lower survival (Fig. 3). At stage 2 and 3 the biggest differences between treatments were between NN NG and AN NG, while herbivory had

minimal effect. The same held true for *Plantago* seedlings: small differences at stage 1, and more pronounced differences at later stages (Fig. 3). The lack of flowering in the AN FG plots of stage 2 appears inconsistent with the other treatments, but it might also indicate the adversity of natural conditions at that stage for juvenile *Plantago*. Overall, explained variation

was low for both mature (25%) and juvenile *Plantago* (23%; Table 3).

Mature *Artemisia* showed reduced survival in competition plots at stage 1 and 2, while herbivory mainly had an impact in stage 3 (Fig. 3). The marginally significant interaction of competition and herbivory resulted in lower survival of mature plants in NN FG plots at stage 3 (Fig. 3). Patterns are not clear, however, and the variation explained by treatment conditions is relatively low (17%; Table 3). In seedlings, only the interaction of competition, herbivory and stage was significant (Table 3): at stage 1, no differences between treatments were apparent, while at stage 3 competition and herbivory affected survival (Fig. 3). Stage 2 was intermediate, with no herbivory but with competition effects. Data are very stochastic, and treatments only explained 10% of the variation.

In mature *Atriplex*, survival was surprisingly higher in AN FG plots than in any other treatment (Fig. 3). Apparently the presence of neighbours was important to this species, as competition plots generally had higher survival than their adjacent competition-free plots. The impact of herbivory resulted, equally surprising, in higher survival in grazed plots, with the exception of stage 3, where survival was maximal under natural AN FG and under NN NG conditions (Fig. 3). This inconsistency is also reflected in a moderate 22% variance (Table 3). The *Atriplex* seedlings reacted like the other species, with a reduction of survival in competition and herbivory plots, except at stage 3, where they survived best under natural AN FG conditions (Fig. 3). Due to lower survival in the NG plots at stage 3, there is a significant difference among stages (Fig. 3, Table 3).

Discussion

Competition and herbivory

There were few similarities in the response to treatment conditions: concerning flowering, all species consistently reacted negatively to competition and herbivory, without any apparent trend over the three stages. Seedling survival generally decreased with successional age due to the combined effects of herbivory and competition. Mature plants showed no consistency in their response to successional age of the saltmarsh. Survival in the competition-free, fenced plots (NN NG), however, remained fairly constant from stage 1 to 3 for both ages: *Plantago* showed a slight decrease in survival, while in *Atriplex* survival increased slightly, with *Artemisia* being constant (Fig. 3).

Differences in their response apparently concerned the effect of competition. While *Plantago* was very sensitive in its flowering percentage, *Artemisia* and *Atriplex* were far less affected (Fig. 2). Another example can be seen in the grazing impacts on seedling survival: no consistent (or significant) trend derived for *Plantago*, though the other two species were suppressed in their survival at stage 1 (*Artemisia*) and stage 3 (*Atriplex*; Fig. 3, Table 3).

These data suggest that the three species differ in their tolerance to competition and herbivory. The following classification can be deduced: *Plantago*, as a palatable rosette plant, is very sensitive to both competition and herbivory; *Artemisia*, a tall, chemically defended plant (Eissa et al., 1996^[17]; Narjisse

Table 4 Seed bank and cover data for the three species at the three stages. Seed bank data from M. Wolters (unpublished manuscript); cover data from 10 relevés per site (4 m², between the experimental blocks)

		Stage 1	Stage 2	Stage 3
Seed bank (seeds · m ⁻² , 0–10 cm depth)	<i>Plantago</i>	80	0	0
	<i>Artemisia</i>	120	11 000	1700
	<i>Atriplex</i>	0	0	0
Cover (%)	<i>Plantago</i>	1.4	0.3	0.1
	<i>Artemisia</i>	4.8	43.0	36.0
	<i>Atriplex</i>	1.3	0.3	1.1

et al., 1997^[32]), is more affected by competition than by herbivory; and *Atriplex*, a relatively tall, woody plant, is little affected by either condition.

Of the several steps in the generative reproduction cycle depicted in Fig. 1, this study investigated flowering and establishment of seedlings. Flowering of *Plantago* and *Artemisia* correlated well with abundance data (Table 4), indicating that flowering is possibly a limiting step in the cycle. *Plantago* was reported to be prevented from flowering by selective grazing by cattle (Jerling and Andersson, 1982^[26]), but it is also an important plant in the diet of geese (Prop and Deerenberg, 1991^[39]; Van der Wal et al., 1998^[50]) and hares (R. Van der Wal, personal communication). No comparable data exist for either *Artemisia* or *Atriplex*.

The step from flowering to seed set (2. in Fig. 1) and the phase before seed dispersal are also subject to grazing. Waterfowl are known to select for seed-bearing inflorescences of saltmarsh plants (Joenje, 1985^[27]), as the seeds have higher metabolisable energy (Bruinzeel et al., 1999^[9]). Also, stem-borer moths have an impact on seed production in *Salicornia europaea* agg. and *Juncus gerardii* (Ellison, 1991^[19]), and as insects were not kept out by the fence, not all forms of herbivory were excluded in the present experiment.

The seed bank is thus mainly influenced by the percentage of flowering and effectively seed dispersing plants, and by how high the import and export of seeds in relation to water movements are. Huiskes et al. (1995^[24]) conclude that most of the driftline material disperses only weakly, and this was supported by measurements close to our experimental sites, where seeds in the driftline correlated well with the abundance of species in the vegetation (M. Wolters, unpublished data). The transport of seeds thus seems to play only a minor role in explaining local abundance of the target species.

A very important step is the germination of seeds from the seed bank or driftline. Germination is most of all under abiotic control, e.g., salt stress, temperature, light conditions, but both neighbourhood competition and grazing by livestock indirectly influence seed emergence (Bakker et al., 1985^[3]; Bakker and De Vries, 1992^[2]). A higher canopy (with only 30% light availability) reduced, e.g., germination of *Plantago maritima* from ca. 90% to 70% (Bakker et al., 1985^[3]). The effects of hares and geese in counteracting effects by opening the canopy has yet to be evaluated.

Once germinated, seedlings face competition from their neighbours (Fig. 2 and 3) and, due to their relative high palatability, are also favoured over mature plants (generally stronger impact of herbivory on survival of seedlings than on mature plants; Fig. 3).

Overall, flowering and germination seem to be the most important phases where competition and herbivory affect the generative reproduction of saltmarsh plants. Seedling establishment, though described as the most sensitive phase (Bertness and Shumway, 1993^[81]), was relatively less susceptible to our manipulations.

How do flowering and survival rates explain the different abundance of the three species during succession?

Once established, all three plant species are capable of vegetative spread. Nevertheless, new plants germinate and establish not only in the numerous disturbed patches created by ice-soring, floodmarks, sediment deposition, erosion, etc., but also under the canopy of existing vegetation (Vince and Snow, 1984^[56]; Bertness and Ellison, 1987^[5]; C. F. Dormann, personal observation). Accordingly, the seed rain from established plants and the import of seeds by tidal water movements continuously provide the possibility of changes in vegetation structure. Competitive forces are hence commonly described in studies of this environment (Vince and Snow, 1984^[56]; Bertness and Ellison, 1987^[5]; Ellison, 1987^[18]; Bertness, 1991^[4]; Pennings and Callaway, 1992^[35]; Mulder and Ruess, 1998^[31]), making flowering and (seedling) survival an important mechanism in bringing about successional vegetation change. The success in establishment is a prerequisite for becoming a potential dominant competitor and in replacing species presently dominant in the vegetation.

Competition was the most important factor in this experiment: all plants showed reduced flowering under competition and in most cases survival was reduced as well. As reduced flowering also means reduced seed set, competition is an important factor in the production of seeds, and the differences in response to it might explain the abundance of the species at the different stages.

Plantago is an early successional species which responded strongly to competition (Fig. 2). Its low abundance, both in the present vegetation and in the seed bank (Table 4), can thus be partly attributed to the effect of neighbours. Herbivory appeared to be almost equally detrimental, so that even at the low-vegetated stage 1 *Plantago* has difficulties in flowering, as this is the most intensively grazed of the three sites (Table 1). Flowering data match the cover data nicely, and survival data support this, in so far as they have the lowest survival of all species, as also found for the cover data (Fig. 3, Table 4). Seeding survival does not add further information, and seems to be of less interest for the abundance of *Plantago*. Hence, *Plantago* might almost be excluded from stage 2 and 3 by the combined action of competition and herbivory, while low cover at stage 1 might allow a slightly better performance.

Artemisia, as a mid-successional species, shows a strong increase in abundance in the present vegetation, as well as in the seed bank, from stage 1 to 2 (Table 4). This correlates well

with the flowering data under AN FG conditions (Fig. 2), which also show a maximum at stage 2. Here as well competition seems to be the driving factor: flowering in AN plots is dramatically reduced at stages 1 and 3, but hardly effected in stage 2. Herbivory, on the other hand, has strong impacts at stage 1 (where grazing pressure is highest), but not in the later stages, as far as mature plants are concerned. Being still dominant at stage 3, *Artemisia*'s decrease in cover with succession (Olf et al., 1997^[34]) cannot be analyzed with the present data. The establishment of seedlings under natural AN FG conditions decreases with stage (Fig. 3), which is not reflected in the seed bank or the coverage data. As in *Plantago*, seedling survival does not seem to provide further information. Thus, while herbivory and competition limit the distribution of *Artemisia* at stage 1, it is solely competition at the later stages, with herbivory having no noticeable effect, that determines performance.

Atriplex, a late-successional species, was the only species in this experiment with a higher survival in AN FG plots than in controls (Fig. 3). It seems as if *Atriplex* would benefit more from physical shelter of neighbouring plants or other facilitative effects, and suffered less from competition. Positive effects of neighbouring plants were reported for other saltmarsh species, acting by reducing salt or mechanical stress (Bertness and Shumway, 1993^[81]; Bertness and Hacker, 1994^[71]). Neighbouring plants also provide shelter, making them less noticeable to herbivores (Feeny, 1976^[20]) and, resulting in higher survival rates in AN FG plots than in NN FG plots (Fig. 3). This seems to be important at stage 1, where not only survival but also flowering of mature plants showed this pattern. Both high flowering and survival rates of *Atriplex* under natural conditions (AN FG) contradict the low cover and the absence from the seed bank (Table 4). *Atriplex*, as in many other Chenopodiaceae (Piggott, 1969^[38]), is known for its dependence on high nutrient supply, especially under hypersaline conditions (Jefferies et al., 1979^[25]). The nutrient-poor conditions of the early stage (Table 1) and the selective grazing pressure that mature plants experience (Drent and Van der Wal, 1999^[16]) may increase mortality of mature plants to the point of local extinction. As hares turn to feeding on *Atriplex* in times of food shortage, grazing-dependent mortality is a winter phenomenon (Van der Wal et al., 2000^[51]), and was not supported by data from the vegetation period alone (Fig. 3).

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