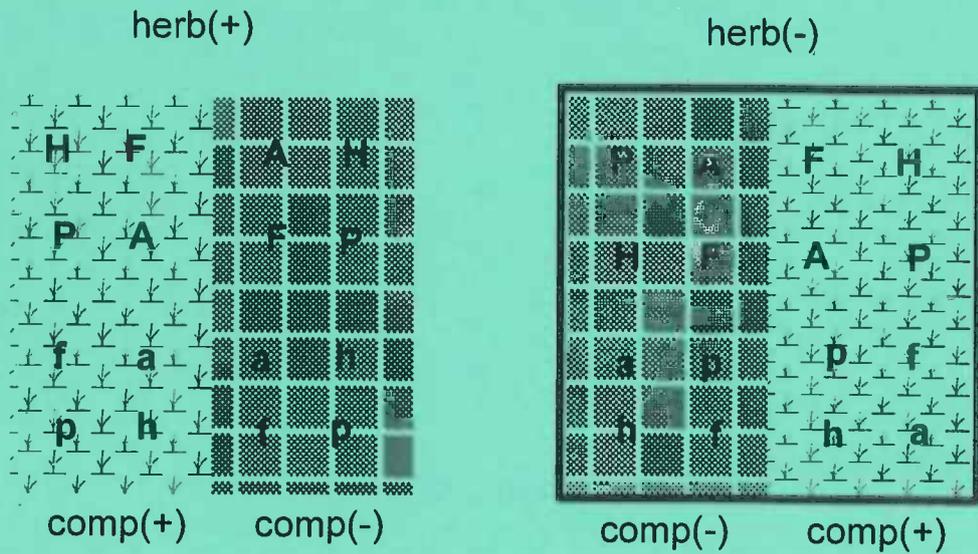


**THE IMPACT OF  
COMPETITION AND HERBIVORY  
ALONG A PRODUCTIVITY GRADIENT**

**AN EXPERIMENTAL APPROACH  
WITH FOUR SALT-MARSH PLANTS**



**Carsten F. Dormann**

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FOUR SALT-MARSH SPECIES**

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# INTRODUCTION

*It is in changing that things find response.* – HERACLITUS

Species composition, species richness and growth forms are observed to vary in a general and predictable way during succession, beginning with species poor colonist communities, leading over diverse grass- and shrub-dominated stages to tall- but slow-growing woodlands (Connell & Slayter 1977, Noble & Slayter 1980, Glenn-Lewin & Van der Maarel 1992). This has caused a wide interest in the factors producing these patterns. Ecologists agree on plant competition, herbivory and physiological stress to vary with system productivity (Grime 1973, 1979, Tilman 1986, 1988, Coley 1987).

In the course of primary succession, the driving factor of species replacement is mostly the accumulation of nutrients, either autochthonous by humus accumulation (e.g. Cowles 1899, Olsson 1958; Olf et al. 1993, Gerlach et al. 1994), or allochthonous, by weathering of substratum (e.g. Cooper 1923, 1939) or clay sedimentation (e.g. Roozen & Westhoff 1985, Olf et al. 1997). Consequently, primary succession is usually accompanied by an increase in productivity and standing biomass (Bazzaz 1979, Pickett et al. 1987). This allows to transfer the literature on biotic interactions along gradient of primary productivity (e.g. Van de Koppel 1997) to primary succession. As productivity is commonly measured as peak standing biomass, I will use the terms synonymously.

There are contradicting views on how the intensity of competition changes with increasing productivity: Newman (1973) and Tilman (1985, 1988) predicted competition intensity to remain constant, with a qualitative shift from competition for nutrients in early stages of succession (= low productivity) to competition for light in later successional stages (= high productivity). Grime (1973, 1979) argued that in unproductive habitats overall competition is low and increases with standing biomass. Support for the former comes for instance from the studies of Wilson & Tilman (1991, 1993) and Reader et al. (1994), while the latter is supported by observations that competitive ability is related to plant biomass (Gaudet & Keddy 1988, Keddy 1989), leading to intense competition at productive sites. Up to now, "the few available data from natural and experimental productivity gradients are conflicting" (Goldberg & Barton 1992, p.780). As Grace (1995) pointed out, much of this conflict might be clarified when scientists would agree on how to measure competition intensity, either in terms of *absolute* biomass reduction (as favoured by Grime) or in terms of *relative* biomass reduction (favoured by Tilman).

Tilman's resource-ratio-hypothesis (1982, 1988) was a major step to a mechanistic explanation of succession, which assumes plant species to be superior competitors at a characteristic set of resource conditions, e.g. to low light and high nitrogen (= low light-nitrogen-ratio). As the ratio of the resource availabilities changes during succession, species replace each other. The model incorporates herbivory only as a "loss constant" (Grace

1990), however, and thus assumes it to be constant over successional stages (or productivities). Grime (1979), and especially Oksanen et al. (1981), expect herbivory to increase in importance with biomass available. As soon as herbivore biomass supports a third trophic level, i.e. carnivore predators (Oksanen et al. 1981), or as food quality for herbivores declines (Van de Koppel et al. 1996), their models predicts a decrease in herbivore impact. Experiments assessing these theories have provide evidence for both tendencies: Herbivore impact increased (Rice 1987, Reader 1992) and decreased with plant biomass (McAuliffe 1986, Ellison 1987).

Experiments manipulating both competition and herbivory are as abundant from marine environments as they are scarce from terrestrial systems. The former are characterised by a multitude of indirect effects, cascading through all trophic levels (e.g. reviews of Menge & Farrell 1987 and Menge 1995), making the interpretation of results an intellectual challenge (Diamond & Case 1986). Too few field studies are available for terrestrial systems to conclude about the importance of competition versus herbivory (Louda et al. 1990, Goldberg & Barton 1992). Those studies have shown, however, that the impact of herbivores might enhance as well as retard succession (Davidson 1993, Crawley 1997), and that herbivores might intensify competitive differences or smoothen them (Dobson & Crawley 1993, Bonser & Reader 1995, Huisman et al. 1997).

Salt marshes are ideal for the examination of structuring forces: The vegetation harbours only a few plant species and, in the case of some back-barrier salt marshes, no direct human impact confounds or overrules natural processes. Despite the harsh environmental conditions, competition is reported to be a relevant structuring factor (Bertness & Ellison 1987, Ellison 1987, Bertness 1991, Huisman et al. 1997). Natural herbivores are abundant on the Wadden Sea salt marshes either as migratory birds (Brent, Barnacle and Greylag Geese) or as resident lagomorphs (hares and rabbits). Carnivores are most of the time scarce.

The study presented here aims at quantifying the importance of competition and herbivory at three early stages of a salt-marsh succession. Particularly, the influence of above-ground grazing and competition by neighbouring plants on plant survival, plant biomass and flowering is investigated. Four common salt-marsh plants were used as target species in a transplantation experiment performed at three successional stages that differ in productivity. With this experiment, the following questions are addressed:

1. What is the impact of competition and herbivory on plant performance? Will competition and herbivory indices show a trend along the productivity gradient?
2. Do the four plant species investigated react consistently to the treatments? And, in case not, can differences be explained by plant adaptation strategies?

Having answered these question, it might be possible to transfer the result to the specific conditions of the salt marsh, and thus to assess what the implications of competition and herbivory are for salt-marsh succession.

# SITE DESCRIPTION

## *THE SALT MARSH OF SCHIERMONNIKOOG*

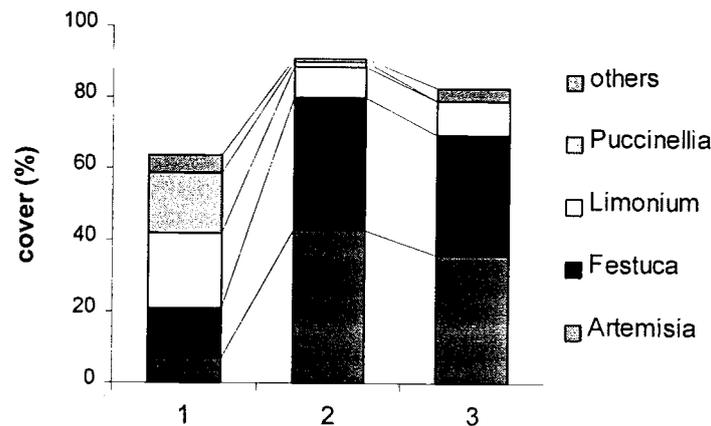
The salt marsh of the island Schiermonnikoog, the Netherlands, has been intensively investigated since the early 1970s (Bakker 1989) for at least the following reason: Accretion of sand, and thereafter clay, leads to a continuous eastwards extension of the island. The age of the island, and accordingly its vegetation, is increasing from 0 years in the East to over hundred years in the West (e.g. Olf et al. 1997). The establishment of the eastern salt marsh can be tracked back until 1809 (Kers et al. 1998). Before that time the eastern part was a sandy beach with small dunes, just like the easternmost hook now.

Eastwards moving currents of the North Sea accumulate sediments on Schiermonnikoog (Bakker et al. 1997). Along the northern beachline, sand is deposited by the sea and blown eastwards by westerly winds, building a sand plate at the islands easternmost end. On the wind- and wave-sheltered backside of the island, calm waters allow fine sediment to settle during tipping high tides, thereby creating a clay layer on top of the sandy subsoil. Comparing the same height above Mean High Water (MHW), say +30 cm, one finds increasing thickness of the clay layer from 0 cm in the East to more than 60 cm in the 150 years old western salt marsh (Olf et al. 1997, Van Wijnen & Bakker 1997). The fine marine deposit provides a nutrient-rich soil (Gray 1992), with the sole exception of nitrogen (Van Wijnen & Bakker 1997). The total N-content of the soil increases with increasing clay-humus-layer in a linear relation (Olf et al. 1997, Van Wijnen & Bakker 1997). The systems productivity increases slowly with the clay layer, after a steep increase during the first years of succession, as shown by Van der Koppel et al. (1996).

The salt marsh represents therefore different age stages with different status in successional development, and form a so-called chronosequence (Pickett 1987, Bakker 1989, Olf et al. 1997). In replacing temporal species replacement through spatial, research can be carried out simultaneously at different successional stages. (A general criticism of space-for-time-substitution and its underlying assumptions is provided by Pickett 1987.)

## *THE VEGETATION*

The development of vegetation during succession is sometimes mistaken with the change in species composition moving to higher elevations at the same age stage. Zonation cannot generally be taken as a successional pattern, especially not on island salt marshes, where succession is related to higher nutrient availability, while zonation to inundation frequency (De Leeuw et al. 1993).



**Figure 1.** Plant species composition at the three experimental sites of 15, 30 and 45 years old, respectively. Relevés of 4 m<sup>2</sup> were made in late June (Nomenclature follows Zffk 1997).

The most dramatic changes take place during the first 50 years of succession (Olf et al. 1997): The species composition changes from a relative species-rich *Puccinellia-Limonium* dominated vegetation to low-diverse stands with *Artemisia* and *Festuca* as matrix plants (Figure 1; Huisman et al. 1993). These two species compete with each other for dominance through the later stages, until *Elymus athericus* outcompetes both of them at a developmental age of higher than 125 years (Olf et al. 1997). Vegetation height and productivity in terms of standing live biomass gradually levels off thereafter, but litter continues to accumulate for further 40 years (Table 1; Van de Koppel et al. 1996, Van Wijnen et al. in prep.). Therefore, three stages of about 15, 30 and 40 years of developmental age were chosen for the experiment (referred to as stage 1, 2 and 3, respectively). The even younger stage (about 5 years old) being almost bare and with instable soil conditions, and the older stages being too little different to be worth examining in this context. The vegetation as such shows an obvious change from stage 1 to stage 2 and 3, the difference between the latter being only slight: About all characteristics of vegetation measured differ between stage 1 and the latter two, but do not between stage 2 and stage 3.

**Table 1.** Characteristics of the vegetation at the three age stages (see also Figure 1), sample standard errors (SSE) are given in brackets. Nitrogen content was calculated from clay layer thickness, using formula 8. N = 10, except for biomass and litter: N = 5. Different letters indicate significant differences within columns at  $p < 0.05$ .

Stage (and corresponding age)	Above-ground live biomass (g·m <sup>-2</sup> )	Litter (g·m <sup>-2</sup> )	Number of species	Vegetation height (cm)	Bare soil (%)	N-content of the soil (g·m <sup>-2</sup> )
1 (15 y)	316 (46) a	48 (21) a	11 (0.37) a	11 (0.5) a	37 (2.7) a	207.65 (4.6) a
2 (30 y)	545 (18) b	157 (36) b	7 (0.50) b	17 (1.15) b	0.6 (0.2) b	381.98 (7.1) b
3 (40 y)	513 (83) b	271 (50) c	7 (0.43) b	20 (0.76) c	0.6 (0.3) b	354.43 (7.0) c

**Table 2.** Comparison of plant characteristics of the four target species.

Species	Life strategy <sup>1</sup>	main storage organ	Growth form	Palatability <sup>2</sup> (consumed organ)	Average cover at stage <sup>3</sup>		
					1	2	3
<i>Artemisia</i>	SC	tap root	shrubby forb	low (stem basis; young leaves)	5%	43%	36%
<i>Festuca</i>	SC	root system	grass	high (leaves, fruits)	14%	38%	34%
<i>Halimione</i>	SC	stem and shallow roots	shrub	occasionally high (leaves, stem)	1%	1%	1%
<i>Plantago</i>	S	tap root	rosette forb	high (leaves, roots)	1%	0.5%	--

<sup>1</sup>determined following Grime et al. 1988; S = stress adapted species, SC = stress adapted competitor

<sup>2</sup>according to Prop & Deerenberg 1991, Snel 1994, Timmerman & Wolff 1996; geese feed only on *Plantago* and *Festuca*, hares make use of all plant species.

<sup>3</sup>10 Relevés per stage; see *Additional Measurements*

The vegetation becomes more monotonous during succession, indicated by a decreasing Shannon's diversity index, less bare soil and more litter (Table 1).

## THE PLANTS AND THEIR HERBIVORES

Four species have been chosen for the experiment: *Artemisia maritima*, *Festuca rubra*, *Halimione portulacoides* and *Plantago maritima* (referred to hereafter with their genus name only). They were chosen for being common salt-marsh plants, while differing in respect to cover, palatability, growth form and life strategy (Table 2).

As shown above (Figure 1 and Table 1), *Artemisia* and *Festuca* are matrix species (dominant in terms of cover as well as biomass), as can be *Halimione* in slightly lower sites (about +20 cm MHW, Van Wijnen et al. 1997). 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) and *Festuca* is growing dense but low turfs, *Artemisia* and *Halimione* are shrubby, taller growing plants. *Festuca* and *Plantago* are common food plants of the geese that forage on the salt marsh during spring staging (Prop & Deerenberg 1991). *Festuca*, *Halimione* and *Plantago*, and sometimes *Artemisia* as well, are all browsed by hares, the main native herbivore of the system (Snel 1994, Van der Wal 1998).

On Schiermonnikoog, Brown Hare (*Lepus europaeus* Pallas) has been hunted by man until recently (1993). Being now protected by nature conservation policies, they seem to become more common. The counted population size in the salt marsh amounts to about 550 individuals, probably far more, in an area of roughly 500 ha (Bestmann & Keizer 1996). Their homerange –having no fixed sleeping site, they forage and rest in a system of overlapping territories– reaches from the dunes down to the lower salt marsh (Timmerman

& Wolf 1997). Their food mainly consists of *Festuca* and *Juncus gerardi*, but they are also found to graze down patches of *Halimione* (Van der Wal 1998). In times of food shortage they may as well make use of the stem basis of *Artemisia*, avoiding roots and leaves (pers. observ.).

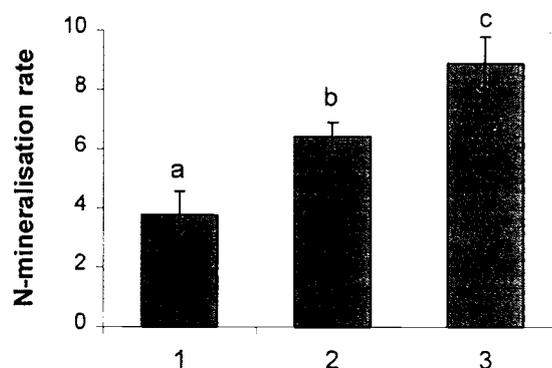
Rabbits (*Oryctolagus cuniculus* L.) are similar to hares with respect to feeding habits. Their occurrence is more restricted to the dunes and the adjacent salt marsh, as their burrows are located there. They can be assumed to be of negligible impact on the lower salt marsh, where no rabbit dropping was encountered during this experiment.

Barnacle Geese (*Branta leucopsis*) and Brent Geese (*Branta bernicla bernicla*), though numerous in early spring (about 7000 and 2500, respectively, dispersed over the salt marsh and adjacent polder fields; Daan Bos & Julia Stahl, pers. com.; pers. observ.) seem to depart too early to have a notable impact on the vegetation of the lower salt marsh in comparison to hares. Barnacle Geese are in addition mainly foraging on the higher elevations, while Brent Geese favour *Puccinellia*, *Plantago* and *Festuca* (Prop & Deerenberg 1991). When the Brent Geese leave in the end of May (Barnacle Geese already leave mid to late April), it is still early in the season for vegetation of the lower salt marsh.

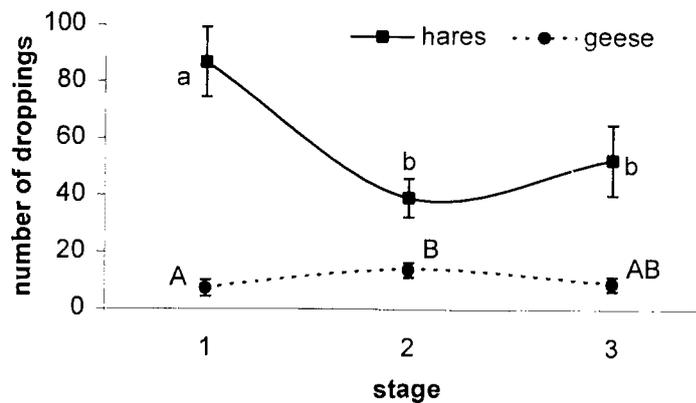
## SETTING THE STAGE: THE FACTORS UNDER MANIPULATION

### *Nutrient availability at experimental sites*

Total N-content of the soil is closely correlated to the thickness of the clay layer (Van Wijnen & Bakker 1997). For plant productivity, however, the N-supply rate might be more important than the total nitrogen pool. Apart from atmospheric deposition (about  $45 \text{ kg}\cdot\text{h}^{-1}$



**Figure 2.** Nitrogen supply rate by mineralization ( $\pm 1$  SSE) at the three sites calculated from biomass data. Nitrogen mineralization rate is given in  $\text{g}\cdot\text{m}^{-2}$  for the top 50cm of the soil (see formula (9)). Different letters indicate significant differences (LSD contrast).



**Figure 3.** Grazing pressure by geese and hares at the experimental sites expressed as numbers of droppings ( $\pm 1$  SSE) counted during the experiment in the 4 m<sup>2</sup> dropping plots. Different letters indicate significant differences between stages (capital letters for geese, lowercase letters for hares & rabbits).

<sup>1</sup>·a<sup>-1</sup>, including wet as well as dry deposition; H. J. van Wijnen, unpubl. results), N-mineralization depends on the clay layer thickness, redox-potential of the soil (correlated to flooding frequency), but also on the amount of "potential substratum", i.e. litter and above-ground non-woody plant material (Van Wijnen et al. 1998). Small herbivores influence the N-supply for the plants by reducing the amount of "potential substratum" and probably by reducing mineralization rate due to soil compaction (Van Wijnen et al. in prep.).

The size of the N-pool of the soil according to formula (8) is given in Table 1, while Figure 2 shows the N-mineralization rate according to formula (9), calculated with biomass data.

The discrepancy between total N-content being highest at stage 2, while N supply rate being highest at stage 3, can not be solved in this context. However, it seems reasonable to assume that the higher above-ground biomass is a consequence of a higher productivity, because nearly all above-ground parts die off during the winter, thus live biomass has been produced during the season. An experiment at approximately the same locations two years earlier has shown that nitrogen limitation was detectable in stage 1 and 2, but not in stage 3 anymore (Van der Wal et al. in prep.). This makes a case for nitrogen supply rate being more important than total nitrogen pool.

### *Grazing intensity*

As Figure 3 shows, geese and hares prefer different stages. Goose grazing impact might accordingly be expected to be highest in stage 2, while hares and rabbits might be more influential in stage 1. The graph also roughly depicts the difference in abundance: geese are only present in spring, hares all year around. These results are somewhat in contradiction with expectancy: Geese, preferring *Puccinellia maritima* as main food, would find a more convenient site at stage 1, while hares and rabbits would have a richer harvest of *Festuca* in stage 2, but are more at stage 1.

For hares the following estimation transfers the dropping data to a grazing impact in terms of % production consumed: During the experiment an average of 0.2 droppings per day and  $\text{m}^2$  were left on the dropping count sites. Per year this amounts to about  $365 \times 0.2 = 73$ . Taking an average weight per dropping of 0.15 g, an estimated total of roughly 11 g dry weight was excreted per  $\text{m}^2$ . Taking into account a digestive efficiency of 65%, a total of  $11\text{g} \cdot 100\% / 40\% = 28$  g dry weight biomass was removed per  $\text{m}^2$  and year. This is about 4.5% of peak standing crop (see also Van de Koppel et al. 1996). Though the grazing impact cannot be assumed to be proportional to the percentage removed biomass (Edwards & Gillman 1987), the measured percentage might be high enough to become important for the whole vegetation. The somewhat lower estimates of Van de Koppel et al. (1997b) might result from their broader spatial sampling of droppings, including the lowest salt marsh as well as the lower dunes.

### *Competition intensity*

Vegetation biomass is often used as a relative measurement for competition intensity, as "competition for all resources is most intense when density or biomass is greatest." (Goldberg 1990, p. 40; Gaudet & Keddy 1988). Total above-ground biomass is highest at stage 3 (Table 1), with both total biomass and litter biomass significantly increasing from stage 1 to 3 (total above-ground biomass:  $F_{2, 29} = 15.86$ ,  $P < 0.001$ ; litter:  $F_{2, 29} = 38.56$ ,  $P < 0.001$ ). The differences in above-ground live biomass ( $F_{2, 29} = 2.59$ ,  $P = 0.092$ ) are a trend pointing in the same direction as total above-ground biomass. That means, competition between plants can be expected to generally increase from the early to the later stages.

Light, sometimes assumed to be the second most probable limiting resource (Tilman 1988, Huisman et al. 1997), will be less available in high and dense vegetation. Light availability is shown in Figure 7 for the three stages. The slope of the curve is closely correlated to vegetation height ( $P < 0.001$ ;  $R^2 = 0.724$ ;  $N = 60$ ). Vegetation height can therefore be taken as a good estimator of light conditions. If biomass and light indeed do determine competition intensity in the mentioned way, competition will be most pronounced at stage 3, and least at stage 1.

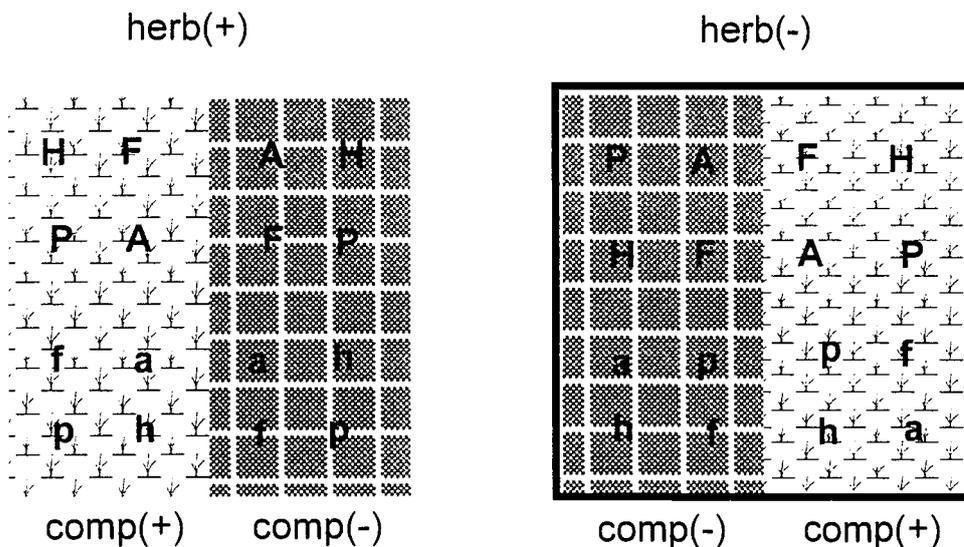
# METHODS

## *THE EXPERIMENTAL SET-UP*

The experimental design consisted of a full-factorial manipulation of herbivory and competition, with 10 replicated blocks at each of three different age stages. Both seedlings and mature plants of the four test species were transplanted into the prepared plots as target individuals.

To manipulate herbivory, the plots were fenced with chicken wire (4 cm mesh size, 50 cm high: herb(-)), or remained unfenced (herb(+)). Herb(+) and herb(-)-plots were kept some meters apart, not to let the herbivores on the herb(+) treatment be deterred by the cages. Competition was attained by transplanting the target individuals into the vegetation present at the experimental plots (comp(+)), while for the no-competition treatment (comp(-)) all above-ground vegetation was removed with electric hand shears and the borders of the plot were trenched to a depth of about 30 cm with a knife, to sever rhizomes of adjacent plants. To reduce loss of soil water content through evaporation, green garden meshes were fixed on the cleared plot, leaving a hole in the centre to place the target individual. Re-growth of the cutted vegetation was eliminated by manually weeding every other week for the whole experimental period.

The four different mature and juvenile specimen were grouped together randomly in a subblock (Figure 2). Two subblocks (comp(+)) and comp(-)) were combined to be fenced (herb(-)) or not (herb(+)).



**Figure 4.** Lay-out of the experimental set-up. This block was replicated 10 times on each of the three stages. On the left hand side, the grazed herb(+) plot, the ungrazed herb(-) plot on the right. The different shadings within the herbivory plots refer to competition (plants indicated) and competition-free conditions. Letters refer to transplanted species, with capital letters for mature plants, and lower case letters for seedlings. The length of block is approximately 1.2m.

The seedlings of *Artemisia*, *Festuca*, and *Plantago* were raised from seeds in the greenhouse, while the *Halimione*-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 Ø, 12 cm deep) and the individual plants were washed out and separated manually, thus being transplanted without adherent soil. *Festuca* was transplanted in turfs of 8 cm Ø and 10 cm depth, which were taken out of the soil using 20 cm PVC-tubes, the tubes of course being removed before transplanting. The transplanting took place between 15 and 22 April 1997.

### RECORDING PERFORMANCE

Initial biomass and length measurements of 10 additional, randomly chosen plants (5 turfs in case of mature *Festuca*) were recorded during the transplanting. Plants were separated into above- and below-ground biomass (in case of mature *Halimione* and *Artemisia* into leaves, stem and roots) and length of the largest leaf was determined (total above- or below-ground length in case of juvenile plants; for mature *Festuca* and *Halimione* total length and additionally number of leaves or tillers, respectively). Then, plants were washed, dried at 70°C for about 48 hours, and weighted to the nearest milligram.

Final harvest of the surviving plants took place between 23 and 30 September 1997. Plants were excavated, transported to the field station and stored in the deep-freezer until further processing. De-frozen plants were rinsed in water and separated into leaves, other above-ground parts, and roots. Only roots attached to the above-ground parts were incorporated, and most fine roots were washed off, resulting in only a slight underestimation of the actual weight. The plant parts were dried at 70°C to constant weight (approximately 48 hours) and weighted to the nearest milligram.

Plant survival was determined on 25 April and around 11 May 1997. Dead plants were replaced. Length of all plants, flowering, bite marks and survival were recorded at the beginning of June, July and at the final harvest (for exact dates see Table II in the appendix). Mortality rates were calculated by dividing the number of plants that died during the respective period by the number of plants alive at the beginning of that period. For total mortality, every plot, in which a plant died, was counted only once, accordingly  $N = 120$ .

For the interpretation of competition and herbivory effects along the age and biomass gradient, indices according to Grace (1995) and Markham & Chanway (1996) were calculated. For further comments on the interpretation of these indices see box 1 in the results.

The absolute competition index ACI is defined as:

$$ACI = \text{weight in comp(-)} - \text{weight in comp(+)} \quad (1),$$

the absolute herbivory index as:

$$\text{AHI} = \text{weight in herb}(-) - \text{weight in herb}(+) \quad (2),$$

and the combined effect is depicted as the absolute competition-herbivory index ACHI:

$$\text{ACHI} = \text{weight in herb}(-)\text{comp}(-) - \text{weight in herb}(+)\text{comp}(+) \quad (3).$$

For the relative competition index RCI, the ACHI is divided by the weight in the no-competition treatment:

$$\text{RCI} = \frac{\text{weight in comp}(-) - \text{weight in comp}(+)}{\text{weight in comp}(-)} \quad (4).$$

To let RCI range between 1 and -1, always the weight of the heavier plant is chosen as denominator. Hence, when the plant in the comp(+)-plot is heavier than the one in the comp(-)-plots, the weight of the plant in the comp(-)-plots is chosen for the denominator. Positive values mean that the target plant suffered a reduction in biomass, while negative values indicate facilitating effects of the treatment. An RCI = 0.6, for instance, has to be interpreted as a 60 % reduction of biomass by competition.

The relative herbivory index RHI is analogously defined as:

$$\text{RHI} = \frac{\text{weight in herb}(-) - \text{weight in herb}(+)}{\text{weight in herb}(-)} \quad (5)$$

(Analogously, the weight of the heavier plant is chosen as denominator.)

The relative competition-herbivory index RCHI is defined as:

$$\text{RCHI} = \frac{\text{weight in comp}(-)\text{herb}(-) - \text{weight in comp}(+)\text{herb}(+)}{\text{weight in comp}(-)\text{herb}(-)} \quad (6)$$

(Here as well, the weight of the heavier plant is chosen as denominator.)

The relative competition-herbivory index serves as an indicator of the added effects of both competition and herbivory (Bonser & Reader 1995).

To allow a comparison among mature plants and seedlings, growth rates ( $r$ ) according to Wilson & Tilman (1991) are calculated, correcting for differences in initial weight:

$$r = \frac{\ln(\text{final biomass in mg}) - \ln(\text{initial biomass in mg})}{d}, \quad (7)$$

where  $d$  denotes the number of days between start and end of the experiment.

### ADDITIONAL MEASUREMENTS

The exact elevation of every experimental subblock was determined using a theodolite. A grid of absolute elevation measurements for the whole island was provided by the National Office for Coastal Protection (Rijkswaterstraat), consisting of a line of wooden poles every 200 m with a known elevation. From there, height measurements of 5 mm accuracy were

**Table 3.** Elevation (cm above mean high water = N.A.P. – 100 cm) of experimental subblocks with minimal and maximal values (sample standard error is given in brackets; N=20). Flooding frequency is approximately 70 times per year (about 10% of all tides), according to Van Wijnen & Bakker (1997).

stage	elevation	
	mean	min / max.
1	31.22	24.7 / 35.7
2	29.70	26.0 / 34.5
3	28.45	24.4 / 35.4

possible (Table 3).

To determine differences in herbivore grazing pressure at the different experimental sites, goose-, hare- and rabbit-droppings were counted weekly in plots of 4 m<sup>2</sup>, 10 per stage. The number of droppings may serve as a measure of the time the animals spent on the plots (Prop & Deerenberg 1991). This is not exactly true for hares and rabbits, as they do not have a constant defecation rate as geese do have and also tend to defecate in latrines. Still, it gives a good estimate of their relative grazing effort (Angerbjörn 1983).

The thickness of the clay layer was determined by taking a soil sample with a soil auger and measuring the distance between soil surface and sandy subsoil to the nearest half centimetre. One measurement per herbivory-block was taken, resulting in 20 measurements per stage. Following Van Wijnen & Bakker (1997), clay layer thickness can be transformed into nitrogen content of the soil using the following equation:

$$\text{N - content (gm}^{-2}\text{)} = 19 (\text{gm}^{-2}\text{cm}^{-1}) \cdot \text{clay layer thickness (cm)} + 125\text{gm}^{-2} \quad (8)$$

On the other hand, nitrogen supply depends on the mineralization rate of decomposable material. For the salt marsh of Schiermonnikoog, Van Wijnen et al. (in prep.) found the following linear relationship between "potential substratum", i.e. litter and non-woody plant parts, and N-mineralization rate:

$$\begin{aligned} & \text{Mineralization rate (g}_N\text{/50cm/m}^2\text{)} \\ & = 0.015 (\text{g}_N\text{/50cm/m}^2\text{/g}_{\text{biomass}}) \cdot \text{biomass (g/m}^2\text{)} - 3 (\text{g}_N\text{/50cm/m}^2) \end{aligned} \quad (9)$$

Relevées of 4 m<sup>2</sup> were made at the dropping count sides in early July, using the decimal scale of Londo (Londo 1976). The vegetation of each experimental comp(+)-plot (140 x 70 cm<sup>2</sup>) was recorded in the same way. For analysis of diversity, these data were transformed into Shannon's index of diversity (Shannon's *H*, hereafter), using the following equation (Begon et al. 1990; p. 617):

$$H = -\sum_{i=1}^N p_i \cdot \ln p_i \quad (10)$$

where *H* is Shannon's diversity index, *p<sub>i</sub>* denotes the cover of the *i*th species (between 0 and 1) and *N* is the total number of species.

Vegetation height (of the relevée plots and the experimental plots) was determined on 3 July 1997 using a Styrofoam disc (30 cm Ø, 60 g), measuring the distance to the soil surface to the nearest centimetre (5 subsamples per relevée).

Above-ground biomass and litter weight was determined by sampling a 10 cm × 50 cm stretch of vegetation in and outside each enclosure (6 replicates per stage) at the time of peak standing biomass, i.e. mid of July. The clipped material was sorted into dead and alive, dried at 70°C for 48 hours and weighted separately.

A lightmeter was used to measure light profiles in late July 1997 in all vegetated subblocks (= comp(+)): 10 photocells of 10 cm × 1 cm each, arranged as a 1 m × 1 cm series, measured light intensity in % relative to reference photocell above the vegetation (wavelength range 400 - 700 nm). The average value of the 10 photocells was recorded every 5 cm from the soil surface upwards, in the centre of the experimental subblock.

## STATISTICAL ANALYSIS

### *Survival and flowering*

Recommended analysis approach of binary categorical data (as dead/alive or flowering/not flowering) is logistic regression (Sokal & Rohlf 1995, Menard 1995). Employing this technique took place in the following manner: All factors were simultaneously entered into the logistic regression model to fit the observed data. The factor with the smallest contribution to the model was excluded in a next step, the model was recalculated and compared to the old. If the log-likelihood-ratio-test indicated a significant improvement, the next factor was excluded until no further improvement could be achieved. This procedure is known as "backward stepwise logistic regression following log-likelihood-ratio-criteria". A factor is significant only, when its removal from the final model results in a significant change in the model. For flowering data, the same approach was chosen, as here also binary data were analysed.

### *Length and biomass analysis*

All data were  $\log_{10}$ -transformed (following the advice of Krebs 1989 and Sokal & Rohlf 1995) to meet assumptions of analysis of variance, i.e. homogeneity of variances and normal distribution of the data. In the same manner as described above, statistically unimportant interactions were removed from the model (backward stepwise), with a removal threshold of  $P = 0.1$  (Crawley 1993). Post-hoc comparisons were made by least-significant-difference-tests. (The recommended Tukey's honest-significant-difference-test proved to be too conservative due to the small sample size and unbalanced data set: Non-parametric tests were in accordance with LSD, but not with Tukey's hsd.)

### *Other*

All other statistics employed ANOVA without removal of factors. Displayed values are mean averages, error bars throughout the report represent  $\pm 1$  sample standard error (SSE). Transformations were conducted when necessary and are given in the text. Light profiles measurements were regressed for each profile separately and slope and intercept of the regressions were analysed by means of ANOVA.

The effect size ( $\omega^2$ , or explained variance) describes how much the respective factor contributes to the total variance in the data set. It can be calculated according to Hays (1988, p. 385) as:

$$\omega^2 = \frac{SS_{factor} - df_{factor} \cdot MS_{error}}{SS_{total} + MS_{error}} \cdot 100\% , \quad (11)$$

where is  $SS_{factor} = df_{factor} \cdot MS_{factor}$ .

$SS$  denotes sum of squares (squared difference of measured value from group mean),  $df$  the degrees of freedom of either the factor or the total model, and  $MS$  denotes the mean sum of squares, thus  $SS_{factor}$  divided by  $df_{factor}$ . This way of calculating effect size reflects the impact of the treatment more realistic than does the conventional way of simply dividing the  $SS_{total}$  by the  $SS_{factor}$  (Hays 1988), because it takes into account the variation within the error term ( $MS_{error}$ ).

To detect trends in the competition and herbivory indices, an analysis of co-variance was employed, using the plant species as factor and the site biomass as co-variable. As the values of the indices range within the interval from  $-1$  to  $+1$ , data were arcsin (square root  $(x + 1) / 10$ )-transformed prior to analysis.

## *METHODOLOGICAL CRITICISM*

When manipulating natural processes, researchers inevitably come into conflict with ecological reliability of their findings. Still, manipulation of natural communities under field conditions offers the most realistic access to ecological processes (Diamond 1986, Aarson & Epp 1990, Gurevitch & Collins 1994). The unexpected implications of vegetation removal

(Aarsson & Epp 1990), trenching (Connell 1990, Bertness & Shumway 1992), caging, watering (not performed in this study), marking of individual plants, use of chemicals (not performed in this study; Bertness 1991) and so forth can not be assessed totally. For the study presented, three main problems of vegetation manipulation emerged:

1. Vegetation removal might have created conditions unlike the ones in plots with bare soil.
2. The use of exclosure and green garden meshes might have deterred or attracted the herbivores.

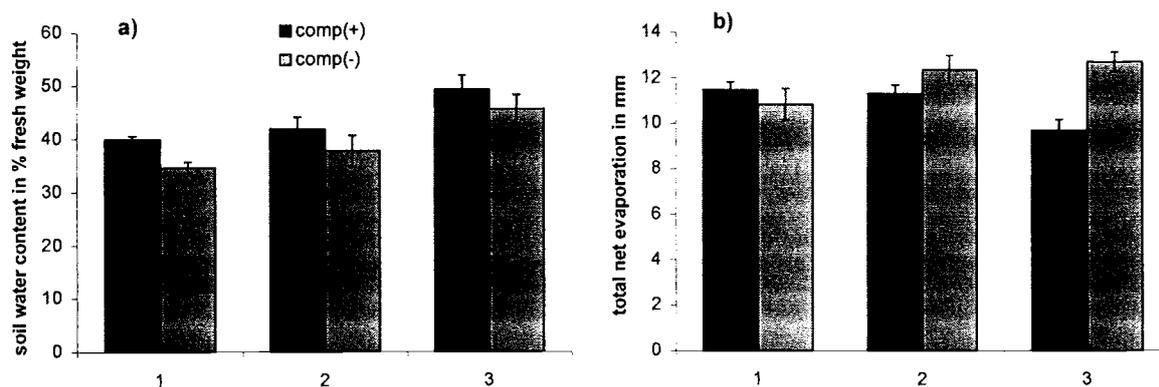
### *Manipulation of Competition*

Competition is often coupled with facilitation effects (Goldberg 1990, Bertness & Hacker 1994): By clipping the vegetation, competition for light and soil resources is reduced, but so is the shelter for the plants, vegetation potentially provides. To experiment with competition and facilitation, different strategies are possible: One could create an artificial vegetation using dense plastic strips to have the full shelter against abiotic impacts without nutrient competition, but which would still cause light interception. As well it is possible to cut off the vegetation and leave the soil bare. This is the most common practice in competition experiments in natural environments (e.g. Goldberg 1987, Aarson & Epp 1990, Bertness & Shumway 1993).

The chosen way is a compromise: In the experiment green meshes were fixed on the comp(-) treatments to reduce soil water loss through evaporation of the soil surface. A seedling, to establish in an open gap in the vegetation, would still be protected by surrounding plants and the litter layer. The mesh is supposed to simulate this: some reduction in mortality without facilitating the target plants when growing higher.

The following two measurements (soil water content and net evaporation) were taken to track the magnitude of difference between the vegetation and the meshes. Soil water content in the vegetation and under the meshes (comp(-)) were determined on the 7 June, 2 July, 22 July and 30 August 1997. The top 4 cm of the soil were sampled by means of a PVC-box (3.5 cm Ø), weighted fresh and after drying to constant weight at 80°C (about 72 hours). Net evapotranspiration (= evaporation - precipitation, serving as an index for the soil-independent water conditions at the different sites) was measured biweekly, using centrifugal vials filled with freshwater, placed under the vegetation and under the meshes. The difference between initial and final weight was transformed into net evaporation values in mm. Whenever tubes were flooded data were excluded from analysis.

The direct measurement of soil water content (Figure 3a) revealed significant differences between competition treatments, between stages, between time periods and showed a significant interaction between time and stage (MANOVA with data from the four sampling times as variables;  $P < 0.001$  for the mentioned effects). The absolute difference between comp(+) and comp(-) is nevertheless not very high, namely maximal 8% (stage 1, June). Interestingly, the wetter stage 1 has the thinner clay/humus-layer, being less able to keep water. Lying on the same elevation as the other stages (Table 3), it is flooded longer



**Figure 5.** a) Soil water content (% fresh weight) of the upper 5 cm soil. For a better conception average of four different sampling times ( $\pm 1$  SSE) are given.  $N = 20$ . b) Average net evaporation ( $\pm 1$  SSE) of water out of plastic vials in the competition treatments at the three stages. Data from flooded vials have been discarded.  $N = 6$ .

and earlier, as the flood arrives stage 1 earlier when surrounding the island from east to west. The fact that soil moisture was always higher in vegetated plots is a common feature of salt marshes (Bertness 1991), whereas in "true" terrestrial plant communities the opposite is the case (Goldberg 1990).

Net evaporation measurements (Figure 3b) dealt with the same aspect as soil water content, i.e. the balance of evaporation and precipitation. These measurements showed a significant effect of competition treatment ( $F_{1, 30} = 7.81$ ;  $P < 0.01$ ) and of the interaction of stage and treatment ( $F_{2, 30} = 6.49$ ;  $P < 0.01$ ). Net evaporation did not differ significantly among stages ( $F_{2, 30} = 1.08$ ,  $P = 0.35$ ). Differences were most pronounced in stage 3, and least in stage 1. Here as well, differences between vegetated and meshed plots were small ( $< 10\%$ ), except in stage 3 (23%). In stage 1 net evaporation was higher in the vegetated plot, while soil water content was lower (Figure 3 a, b). The observed effects of facilitation and higher water content in vegetated plots would occur also under natural conditions, when there are any bare patches (e.g. Bertness 1991, Pennings & Callaway 1992, Bertness & Shumway 1993). Salinity usually increases when the soil is bare (Bertness 1991), but was not measured here. For the soil parameters measured, removal of the vegetation did have an effect, but its magnitude was low, so that experimental conditions can be viewed as being realistic.

### *Manipulation of Herbivory*

The manipulation of vertebrate herbivory by exclosures was successful. No plant in any of the exclosures showed bitmarks from geese, hares or rabbits. In some *Plantago* the traces of insect feeding were found, however. As they were scarce and the wounds not profound, insect herbivory can seemingly be neglected.

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The green meshes of the unvegetated plots unfortunately attracted hares and rabbits to use them as latrines (pers. observ.).

More problematic was the attraction of hares by the green meshes on the comp(-)-plots. Plants in the middle of the green meshes were most probably more apparent than would have been without the meshes. Nevertheless, not all plants in the comp(-)-plots were grazed by hares. The impact of hares is most likely slightly overestimated. Geese, on the other hand, are making less use of the plants in the unvegetated plots, as they are feeding with high peg-rates and the single plant in the meshed plots is likely to be unattractive to them. This might to a certain extent outbalance the higher impact of hare grazing. While on the scale of the whole stage grazing pressure remained the same, herbivores might have concentrated on the plants in the experimental plots. The expectancy that clay deposition would bury and conceal the meshes was only accomplished at stage 1.



# RESULTS

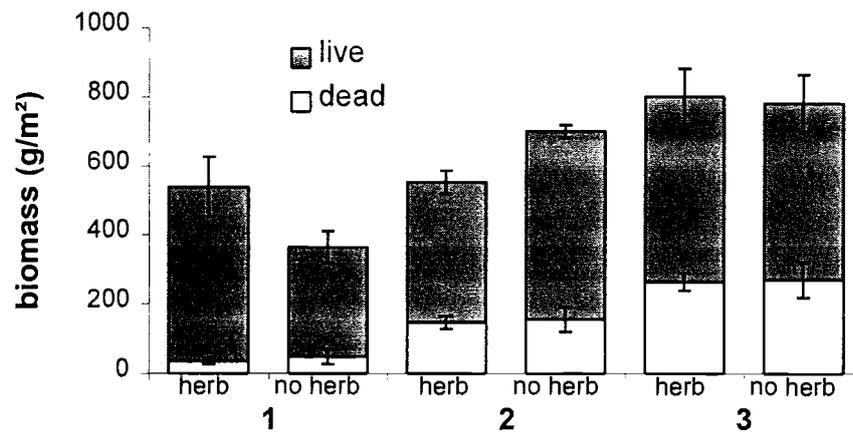
## COMMUNITY RESPONSE TO HERBIVORE EXCLUSION

The exclusion of herbivores resulted in the change of vegetation characteristics within the growing season. These can be compared between the three stages and may indicate the trend of development that vegetation would experience in exclosures on the long run. Table 4 summarises the results of the vegetation response to the short-term exclosure of

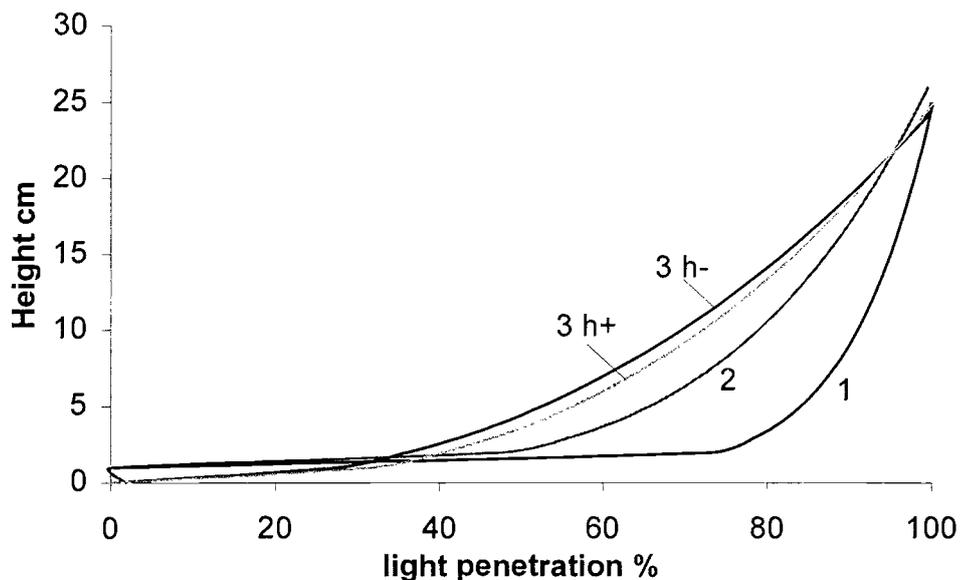
**Table 4.** ANOVA results of different vegetation parameters of the two herbivory treatments at the three stages. Bold printed factors explain significant amounts of the variance of data.

Parameter	Factor	df	MS <sub>factor</sub>	F	p	effect size %
cover	<b>herbivory</b>	1	0.192	5.33	0.0248	4.0
	<b>stage</b>	2	0.758	21.08	0.0000	38.2
	interaction	2	0.092	2.57	0.0861	
arcsin(x/100)-transf.	error	54	0.036			
height	<b>herbivory</b>	1	0.219	22.87	0.0000	10.2
	<b>stage</b>	2	0.657	68.42	0.0000	63.1
	interaction	2	0.003	0.27	0.7628	
log(x+1)-transf.	error	54	0.010			
Shannon's H	herbivory	1	0.006	0.18	0.6770	
	<b>stage</b>	2	0.962	26.78	0.0000	44.5
	<b>interaction</b>	2	0.167	4.65	0.0137	7.0
	error	54	0.036			
slope of light profile	<b>herbivory</b>	1	0.115	8.98	0.0041	4.2
	<b>stage</b>	2	0.803	62.69	0.0000	64.8
	interaction	2	0.017	1.30	0.2800	
	error	54	0.013			
living above-ground biomass	herbivory	1	0.007	0.413	0.5253	
	stage	2	0.042	2.589	0.0923	
	<b>interaction</b>	2	0.080	4.960	0.0140	19.6
	log-transf. error	30	0.016			
dead above-ground biomass	herbivory	1	0.00	0.00	0.9680	
	<b>stage</b>	2	13.20	40.23	0.0000	69.1
	interaction	2	0.02	0.05	0.9479	
	log-transf. error	30	9.84			

Abbreviations: df = degree of freedom; MS = mean sum of squares; F = ratio of MS<sub>factor</sub> and MS<sub>error</sub>; P = probability of type 1 error. Effect size ( $\omega^2$ ; amount of explained variance between treatments) was calculated according to formula (8). Averages of effect size: Herbivory: 3.1%, Stage: 40.4%, Interaction: 9.6%.



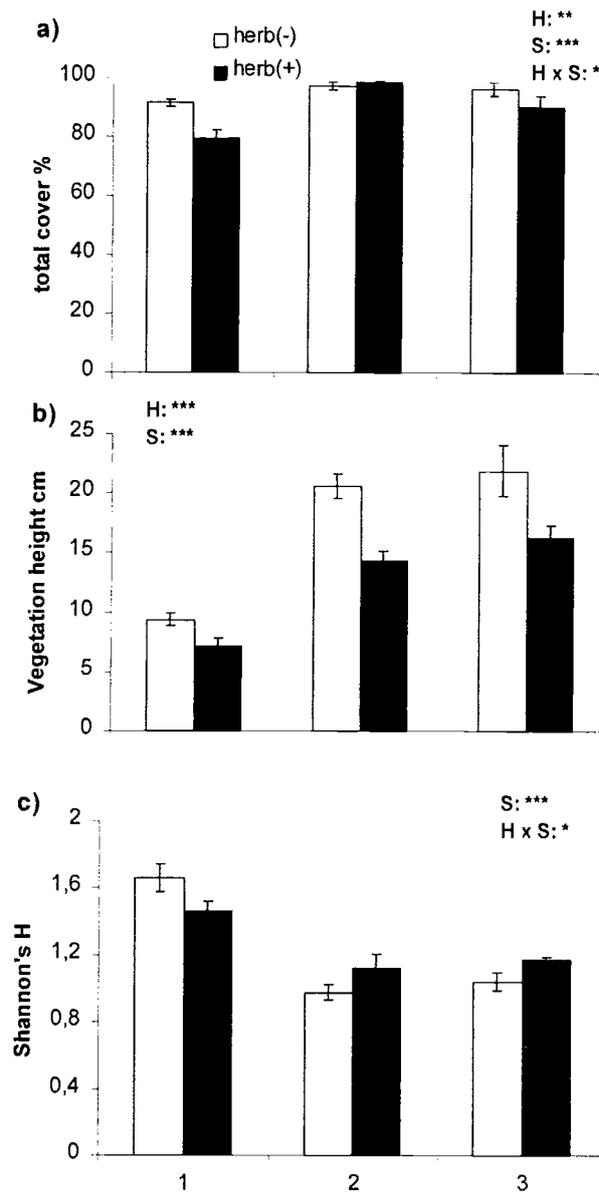
**Figure 6.** Standing above-ground biomass ( $\pm 1$  SSE) at the experimental sites, with and without herbivory. Lower parts of the bars represent litter, upper parts living tissue. Numbers under the abscissa refer to stage.



**Figure 7.** Light profiles for the three stages, showing the percentage of incoming light at the different heights above the soil. Numbers refer to stages, h- and h+ to ungrazed and grazed plots, respectively. Only stage 3 shows a significant difference between the two herbivory treatments ( $P < 0.05$ ), thus only here two lines are given. Profiles are calculated with the power function ( $\text{light penetration} = \text{intercept} \cdot \text{height}^{\text{slope}}$ ) using the average coefficients of regressions. Regressions were highly significant with  $R^2$ -values between 0.80 and 0.94;  $N = 10$ .

herbivores. To give an idea of the importance of each single factor, effect size was calculated, according to Hays (1988). The percentage explained variance can be taken as an estimate of ecological significance of the respective factor.

Vegetation response in terms of biomass yielded obvious results when taking into account only above-ground weights: Standing dead biomass increased continually from



**Figure 8.** The community parameters a) cover, b) vegetation height, and c) Shannon's H of the vegetated part of the subblocks (comp(+)) as a function of stage and herbivory. Significant factors are given above the bars. Error bars indicate  $\pm 1$  SSE,  $N = 10$ .

total cover of vegetation (see above), with a significant impact of herbivores only at stage 1. For total above-ground biomass an impact of stage and the interaction of stage and herbivory was found ( $F_{2, 30} = 15.86$ ,  $P < 0.001$ ), none of herbivory ( $F_{1, 30} = 0.36$ ,  $P = 0.553$ ).

Light conditions differed significantly among stages (Figure 7 and Table 4). For stage 3 a difference between grazed and ungrazed plots could already be detected, in spite of the fact that the experiment lasted only for two months when light profiles were measured. Grazing led to a higher availability of light at all height levels.

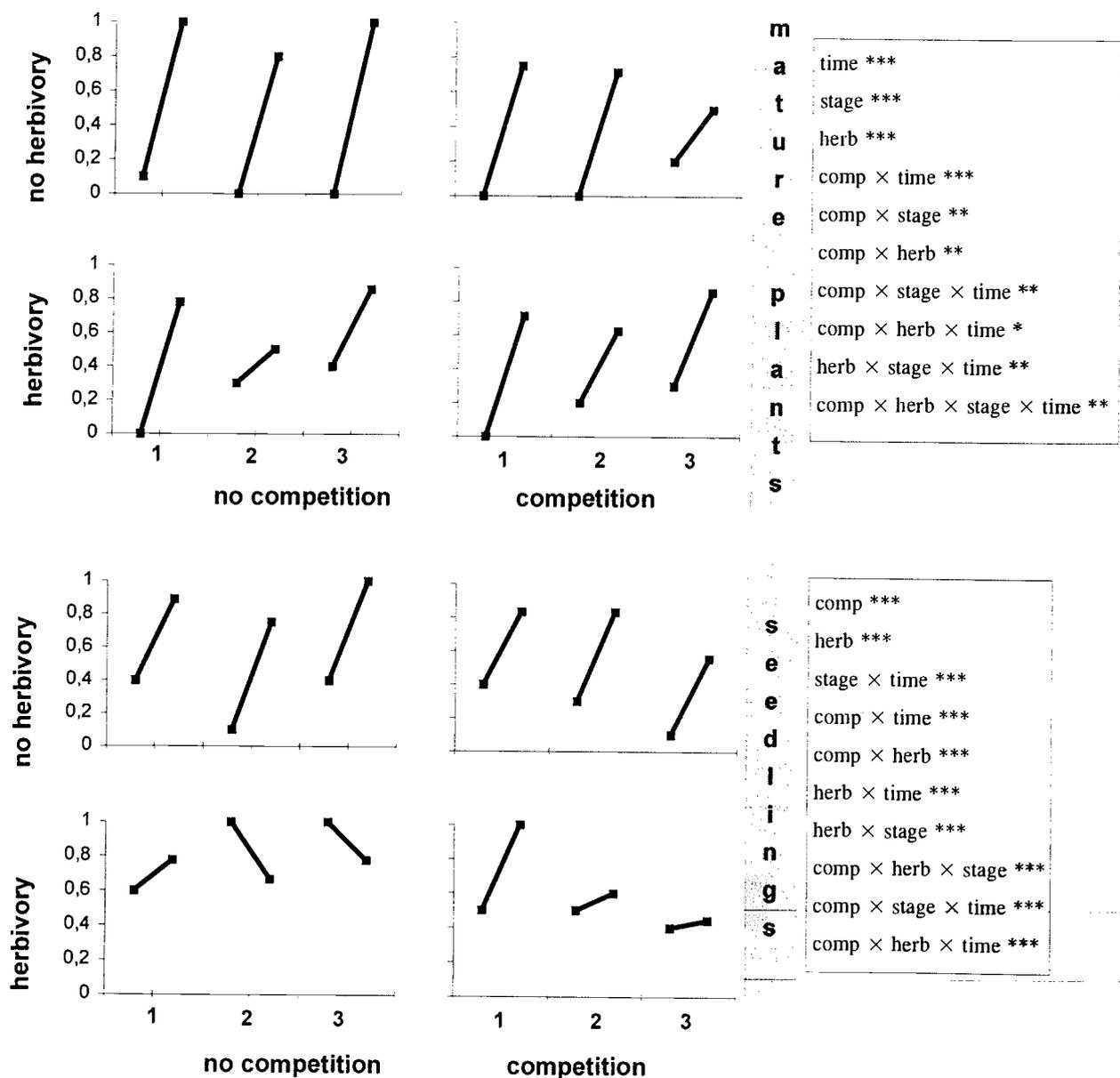
Most obviously, the total cover (of phanerogame plants) differed between treatments and stages. Bare soil was mostly rapidly colonised by mats of green algae. The interaction graph (Figure 8a) shows that herbivory had unlike effects in the different stages, namely that no difference in cover by caging were found in stage 2 while it was reduced outside the enclosures of stage 1 and 3. The main effects were detectable as well (stage:  $F_{2, 54} = 21.08$ ,  $P < 0.001$ ; herbivory:  $F_{1, 54} = 5.33$ ,  $P < 0.001$ ). The actual magnitude of change was small due to the fact that the experiment run only for 4 months when measurements were taken. Grazing intensity by hares was lowest at stage 2 (Figure 3) and vegetation cover seemed to be unaffected there (Figure 8a). There is, however, evidence that grazing did take place (see vegetation height next paragraph). The response in cover was not uniform for all species, but the differences never reached a significant level.

Vegetation height was strongly affected by herbivory ( $F_{1, 54} = 22.87$ ,  $P < 0.001$ ). In all stages plants grew higher inside the enclosure than outside. The difference between herb(+) and herb(-) treatment was highest in stage 2 (Figure 8b). The increase in vegetation height with salt marsh age is shown in the introduction (Table 1).

Stage 1 harboured more species than stage 2 and 3 (Table 1). Accordingly, Shannon's  $H$  was higher there, and decreased significantly towards stage 2 (Figure 9c). While grazing in the older stages increased diversity, it led to a significant decrease at the early successional stage 1.

## SURVIVAL ANALYSIS

Combining period 1 and 2 (15 April - 13 May 1997, see Table II in the appendix) as starting phase and period 4 and 5 (30 May - 1 October 1997) as main phase of the experiment, survival through time was included in the analysis as *time* together with the factors stage, herbivory, and competition and all their interactions, for mature and juvenile plants separately. The survival differed strongly between plant species, stages, grazing treatments, and during time. Table II in the appendix summarises the survival rates at the



**Figure 9.** Survival probability for mature (upper four panels) and juvenile (lower four panels) *Artemisia maritima* plants in the different treatments. Lines connect two time periods within one stage. The left dot refers to the first 4 weeks of the experiment, the right dot to the last 4 months. The boxes give significance level of factors according to logistic regression. \*\*\*, \*\* and \* refer to  $P < 0.001$ ,  $< 0.01$  and  $< 0.05$ , respectively.

three successional stages under control conditions, i.e. comp(+) and herb(+).)

The dramatic mortality in the second period seems to be a result of the weather conditions: While the first period was rather wet and cold (which apparently did not bother the plants too much), the second was cold without any precipitation for 3 weeks (from late April to mid of May). Survival during time changed in *Artemisia*, *Festuca* and *Plantago*, but did not in *Halimione*.

The numbers in Table II (Appendix) might indicate an effect of transplantation or weather. Plants surviving the first month after transplanting showed a survival thereafter of 80 to 90% (period 4 and 5). The high mortality of seedlings is easier to understand when remembering the fact that they were raised in a greenhouse without salt-stress. The die-off of mature *Artemisia* and *Plantago* plants remains nevertheless unexplained.

### *Artemisia maritima*

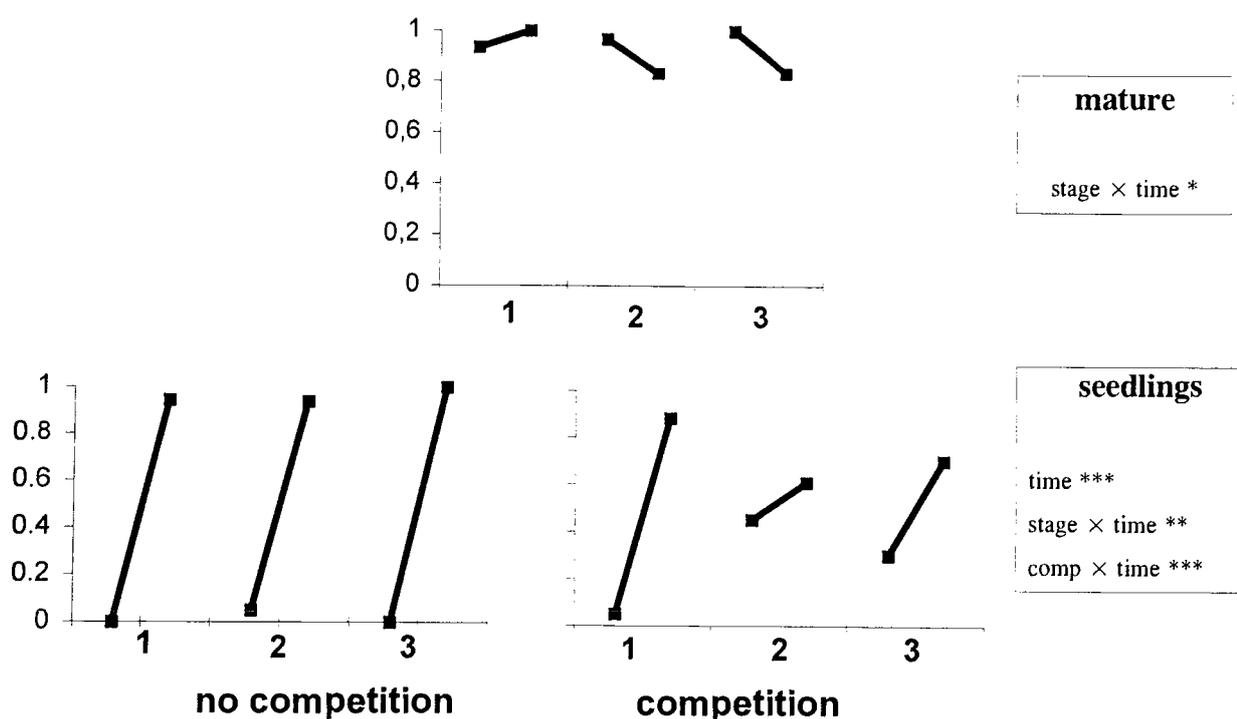
For mature plants, time was an important factor. Under all conditions, survival was higher in the main experimental phase (right dot of the two dots connected). The left graphs do hardly differ from the right, which means that competition is not very important. Only when plots were excluded from both competition and grazing (left, upper panel), survival was notably higher in the main phase. Grazing in the main experimental phase reduced the survival by about 20 % under competition-free conditions (compare the right dots in the upper and lower panel on the left side). Initially, survival was higher though when plots were grazed (both with and without competition. This means that in the beginning herbivory was advantageous for the plants –while competition was of minor importance– but later competition had a strong negative impact (right dots in the two right panels are lower than in the left panels). Survival for mature *Artemisia* seemed to increase with stage, but also depended on the competition and herbivory conditions.

For the seedlings, patterns are very different. Time as a main factor had no significant effect (the connecting lines are relatively short and have both positive and negative slopes). Differences between start and main phase were more pronounced when the plots were not grazed (upper panels have longer lines), and they almost disappeared in stage 2 and 3 when the target species had to face competition (lower right panel). Plants suffered more from herbivory in stage 2 and 3, than in the youngest stage: Survival in the main phase was even lower than in the start phase (resulting in lines with a negative slope). Generally, competition resulted in lower survival, especially during the main phase.

### *Festuca rubra*

Survival of mature plants was high (Figure 10). It decreased slightly through time in stages 2 and 3, while it slightly increased in stage 1. Herbivory and competition were not affecting survival significantly.

Juvenile plants of *Festuca* were affected by competition, time and stage (Figure 10, lower panels). Survival in the absence of competition increased from start to main phase by

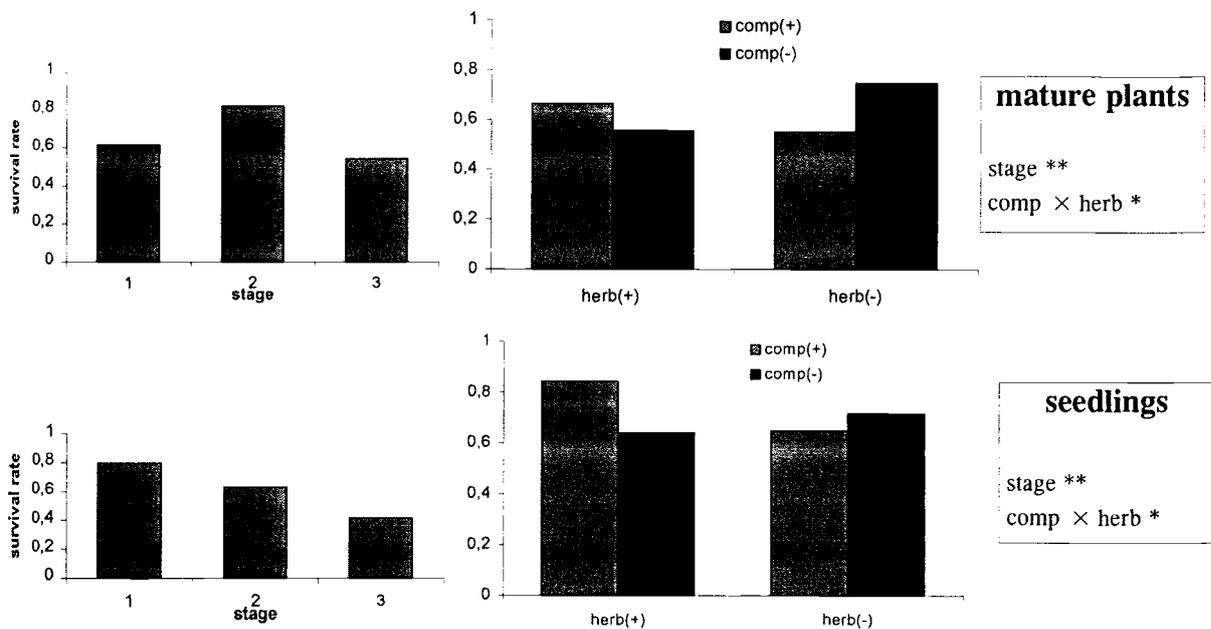


**Figure 10.** Temporal change in the survival rates of mature (upper panel) and juvenile (lower two panels) *Festuca rubra* in the different stages and competition treatments. Lines connect two time periods within one stage. The left dot refers to the first 4 weeks of the experiment, the right dot to the last 4 months. The boxes give significance level of factors according to logistic regression.

90% in all stages. Considering facilitation effects, initial survival was high at the dense vegetated stage 2, while slightly lower at stage 3 and almost no plant survived in the bare stage 1. During the experiment, positive neighbourhood effect shifted to competition in stage 2 and 3, where the increase in survival was far less pronounced than in stage 1. Here, survival probability in the main phase was as high as in the competition-free plots (about 90%). Apparently, competition outbalanced the cessation of adverse abiotic conditions in the older stages.

### *Halimione portulacoides*

No temporal trend in survival could be detected (Figure 10). Stage effects were independent from other factors, for mature plants as well as for seedlings. For the latter survival decreased from stage 1 to 3, while for mature there was an optimum at stage 2 (with the thickest clay layer). The response to the interaction of competition and herbivory was comparable in the two ages: when grazed, competition effects were positive, but without grazing, competition had a negative influence on *Halimione* survival. Especially for the seedlings, herbivory resulted in a higher survival when the plots were accessible for the herbivores. As grazing of the target plant will hardly promote its survival, it seems that grazing of the neighbours allowed the target plants to perform better. In a dense vegetation,



**Figure 11.** Effect of the treatments with a significant impact on the survival of mature (upper two panels) and juvenile (lower two panels) *Halimione portulacoides*. Left: Survival rates between stages. Right: Survival rates in the competition and herbivory plots. The boxes give significance level of factors according to logistic regression.

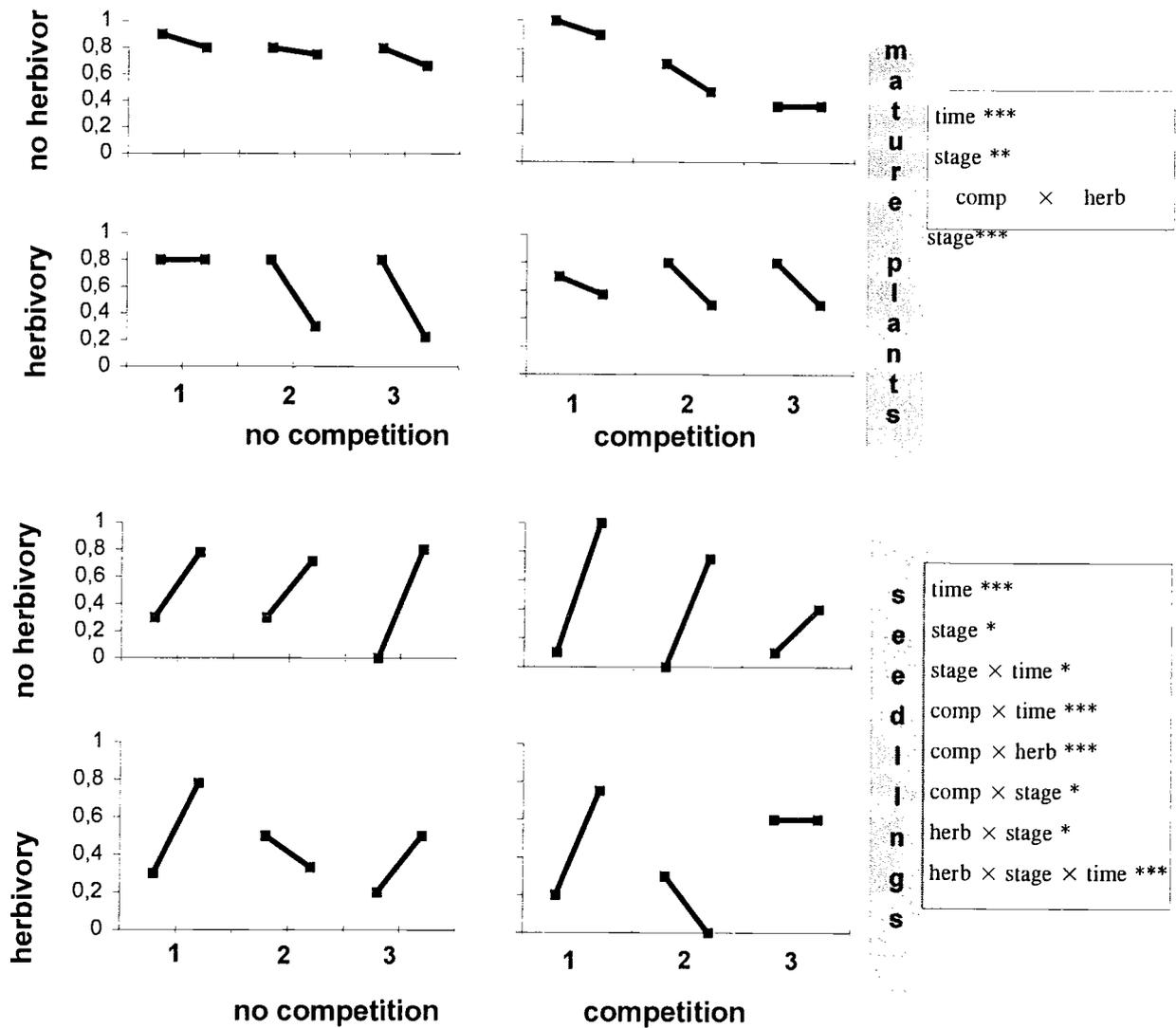
herbivory might thus be positive for the establishment of small plants and seedlings. Whenever plants were standing free from neighbours, herbivory directly affected the target plant and thus reduced survival.

### *Plantago maritima*

Survival of during the two phases of mature *Plantago*-plants differed from juveniles. While for the mature plants survival slightly but consistently decreased, it increased dramatically for the juveniles (Figure 12, lower panels).

Adult survival was highest at stage 1 and hardly affected by competition, but strongly by herbivory (see the right dots, stage 2 and 3, in the lower left panel). The impact of herbivores in the older stages was substantial in the comp(–)-plots and minor in the comp(+)-plots. Plants in the vegetation seem to be less apparent to the hares. Herbivory might thus be a major threat for *Plantago* growing in scare vegetated places.

The picture is more complex for the seedlings (lower panels of Figure 12). Survival increased tremendously in the ungrazed plots (long lines in the upper panels), and in stage 1, despite grazing. In stage 2, grazing resulted in a lower survival in the main experimental phase than in the beginning. Here was the effect of competition additionally lethal to the target species, leading to a total loss of species in that combination of treatments. In stage 1 as well as in stage 3, herbivory prevented competition, and the survival in the vegetated



**Figure 12.** Temporal change in the survival of mature and juvenile *Plantago maritima* plants in the different treatments. Lines connect two time periods within one stage. The left dot refers to the first 4 weeks of the experiment, the right dot to the last 4 months. The boxes give significance levels of factors according to logistic regression.

plots is accordingly as high as in the unvegetated (clearly so for the main experimental phase).

### *PLANT LENGTH*

The analysis of plant length is only given in the appendix, as the phenological variability of the plants is too high to use plant length as a reliable measure of treatment effects.

**Table 5.** Overall ANOVA results of the final biomass for the transplantation experiment. The degrees of freedom (df) for the respective factors are listed in the second column, except for the error term (within + residual), where they are given in parenthesis of the respective means sum of squares (MS) column. For each plant species mean sum of squares, F value (with its significance<sup>1</sup>) and effects size ( $\omega^2$  in %) are given.

Source of Variation	df	Artemisia			Festuca			Halimione			Plantago		
		MS	F	$\omega^2$	MS	F	$\omega^2$	MS	F	$\omega^2$	MS	F	$\omega^2$
WITHIN + RESIDUAL (df)		0.033 (118)		0.034 (151)		0.060 (103)		0.024 (89)					
AGE	1	2.15	64.35***	18.8	2.03	60.28***	21.3	2.78	46.40***	21.5	0.12	5.03*	2.1
COMP	1	2.6	77.91***	22.7	0.078	23.22***	8.1	1.77	29.43***	13.7	1.3	53.01**	24.0
HERB	1	0.21	6.19*	1.6	0.09	2.68 <sup>n.s.</sup>	0.9	0.63	10.38**	4.9	0.86	35.23**	15.9
STAGE	2	0.04	1.05 <sup>n.s.</sup>	0.1	0.03	0.98 <sup>n.s.</sup>	0.6	0.06	1.14 <sup>n.s.</sup>	0.9	0	0.15 <sup>n.s.</sup>	0
BLOCK	27	0.06	1.85*	6.4	0.03	0.93 <sup>n.s.</sup>	8.5	0.08	1.34 <sup>n.s.</sup>	16.7	0.02	0.66 <sup>n.s.</sup>	9.9
AGE×COMP	1												
AGE×HERB	1							0.24	3.92*	1.9	0.17	6.96*	3.2
AGE×STAGE	2												
COMP×HERB	1	0.24	7.04**	1.8	0.13	3.75 <sup>n.s.</sup>	0.1	0.72	12.02**	5.6	0.5	20.29**	9.3
COMP×STAGE	2	0.19	5.7**	2.8	0.09	2.79 <sup>n.s.</sup>	1.9	0.17	2.76 <sup>n.s.</sup>	2.6			
HERB×STAGE	2				0.06	1.64 <sup>n.s.</sup>	1.3				0.1	4.16*	3.7
AGExCOMP×HERB	1												
AGExCOMP×STAGE	2												
AGExHERB×STAGE	2												
COMP×HERB×STAGE	2				0.12	3.44*	2.5						
AGExCOMP×HERB×STAGE	2												
total explained variance				54%			45%			68%			70%

<sup>1</sup> \*\*\*, \*\*, and \* refer to the significance level of  $P < 0.001$ ,  $P < 0.01$ , and  $P < 0.05$ , respectively. <sup>n.s.</sup> indicates non significant factors.

## ANALYSIS OF TRANSPLANT BIOMASS

Results are presented for each of the 4 species separately. Obvious expectations for how the main factors plant age, stage, herbivory, and competition affect the growth of the individual plants are shortly summarised to shorten the presentation of each species.

- **PLANT AGE:** In principle, seedlings should be lighter than mature plants. This is simply due to the fact, that the initial weight of the seedlings was far lower. Relative response to the treatments might on the other hand be stronger, as relative growth potential is higher.
- **STAGE:** Biomass can be expected to increase with nutrient availability, i.e. with the age of the salt marsh.
- **HERBIVORY and COMPETITION:** Both reduce biomass, while the release from each of the factors is expected to result in a biomass increase.
- **BLOCK:** To correct for spatial heterogeneity within stages, a block factor was included. Since it is unimportant for the presentation of plant weights, it is omitted in the presentation.

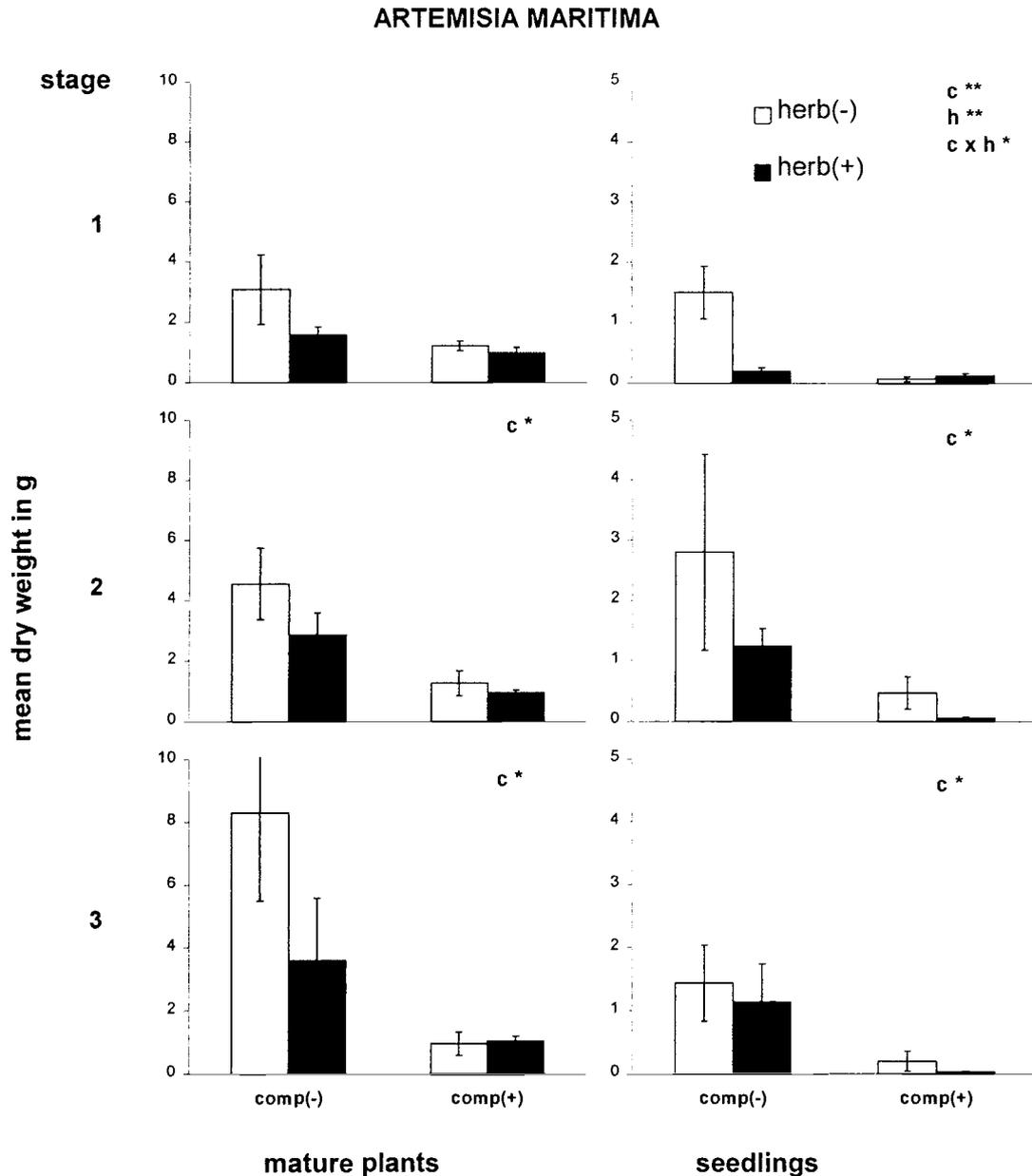
ANOVA-results are summarised in Table 6.

### *Artemisia maritima*

As expected, mature plants were heavier than seedlings. Relative growth rate was higher for juvenile plants though (see: *The Differences between Plant Ages* and Figure 21).

The response to the different treatments was the same for both plant ages, except at the first stage. There, no effect of neither competition nor herbivory on the biomass of the adult plants was detectable, while they (as well as their interaction) were detectable for seedlings. An increase over the stages is apparent, though not significant (Figure 13). In mature plants neither herbivory nor the interaction of herbivory and competition reaches significance (given in the upper right corner of each panel), though herbivory is of significant contribution to variance for all three stages and both plant ages taken together (Table 6). Looking at the competition-free plots only, the biomass shows indeed significant differences between stages (c × s \*\*).

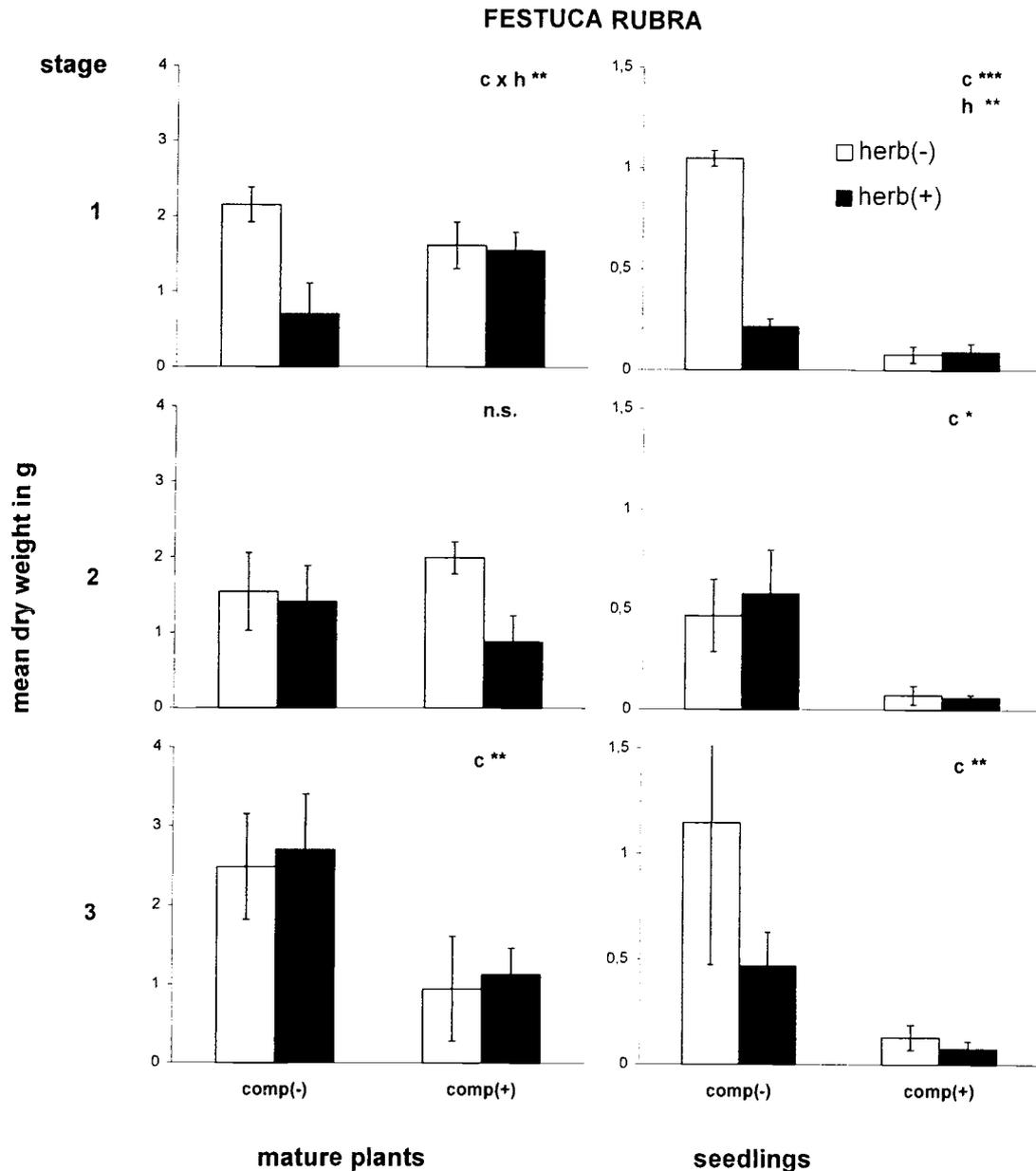
Competition reduced biomass significantly in all three stages, though mainly in the herb(-)-plots. Plants in the comp(+)-plots had less than a third of the weight of the plants in the comp(-)-plots. When herbivory interacted with competition, effects of the latter disappeared (but see stage 2, seedlings, for an exception). Thus, most of the time no effect of competition was measurable when plants were grazed.



**Figure 13.** Average biomass ( $\pm 1$  SSE; dry weight in g) of the transplanted *Artemisia maritima* individuals. From top to bottom stage 1 to 3, left for mature plants, right for seedlings. Note differences in scaling between mature and juvenile plant biomass. Significant effects are given in the upper right corner of each panel. Overall effects are listed in Table 6.

### *Festuca rubra*

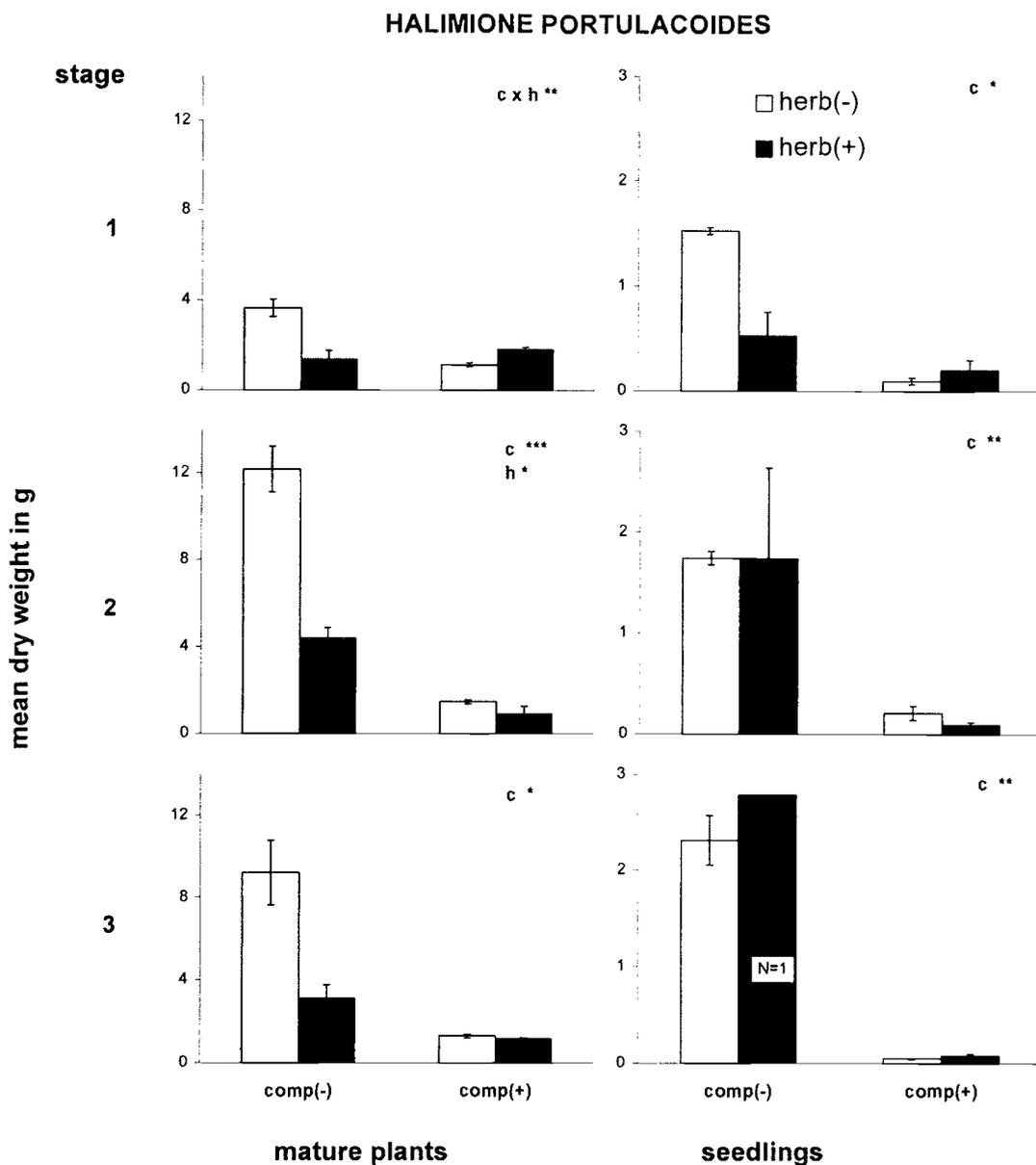
Due to high variation in final weight only age and competition effects were significant in the overall analysis. Successional stage apparently did not influence plant performance (Figure 14). Like in *Artemisia*, herbivore effects were measurable only in comp(-)-plots, and also only in stage 1. Where acting, grazers removed about 60% of mature and 70% of juvenile plants biomass.



**Figure 14.** Average biomass ( $\pm 1$  SSE; dry weight in g) of the transplanted *Festuca rubra* individuals. Note differences in scaling between mature and juvenile plant biomass. For further explanation see Figure 13.

Seedlings seemed to be more susceptible to competition than mature plants: Competition is contributing significantly to seedling weight differences in all stage, while only in stage 3 for mature plants. Biomass of seedlings is reduced to roughly 20% and to about 50% in stage 3 for mature plants.

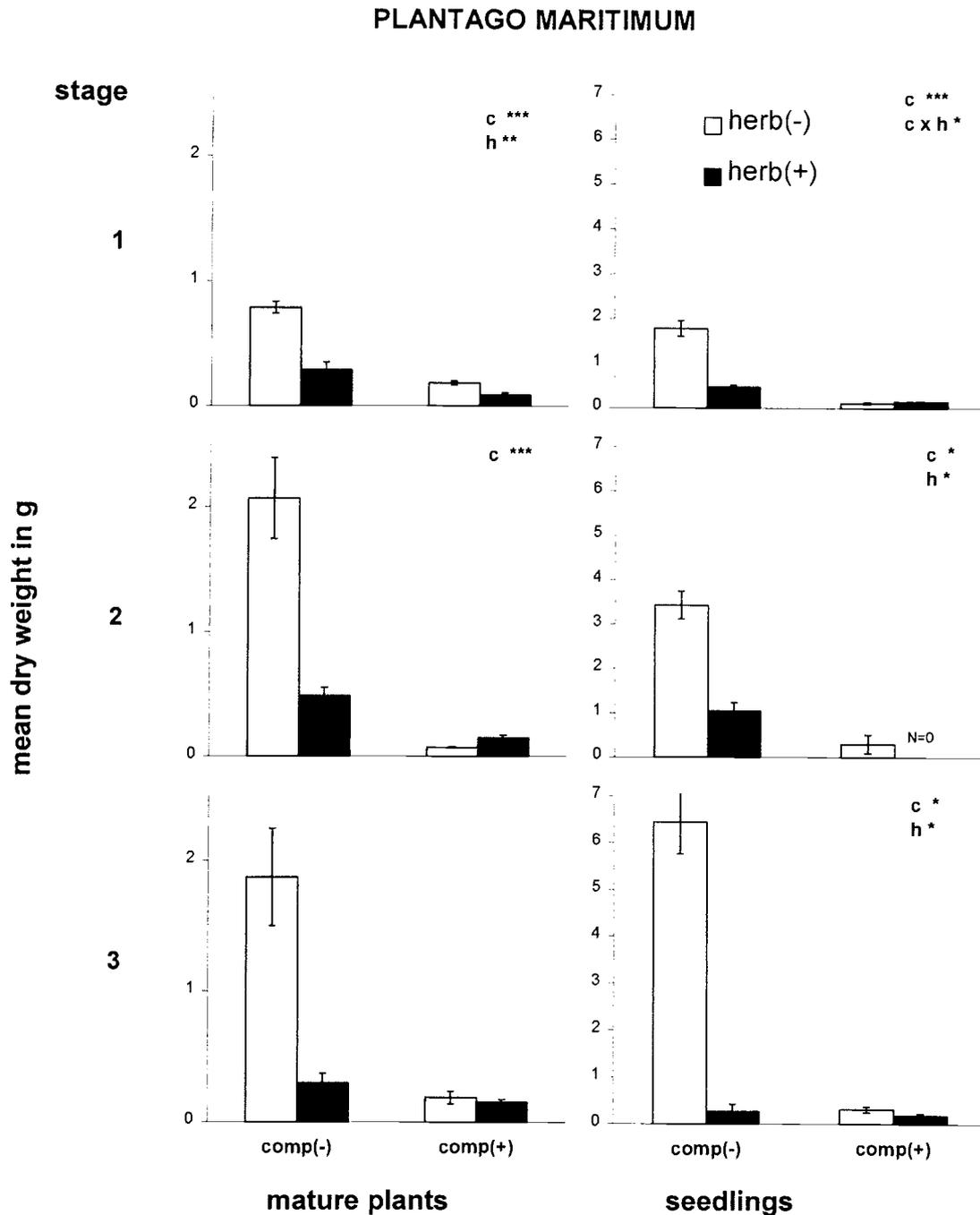
When plants were grazed, differences between competition-treatments were smaller than in the ungrazed controls. Competition nevertheless reduced plant biomass further: Only at stage 1 competition did add no further effect to the grazing.



**Figure 15.** Average biomass ( $\pm 1$  SSE; dry weight in g) of the transplanted *Halimione portulacoides* individuals. Note differences in scaling between mature and juvenile plant biomass. For further explanation see Figure 13.

### *Halimione portulacoides*

As in *Festuca*, biomass is not significantly different between the three stages (Figure 15). In juvenile as well as in mature plants a positive trend seems to exist (though this trend is again restricted to the competition-free grown plants). An effect of grazing was only found for mature plants (overall ANOVA:  $a \times h$  \*\*). Biomass reduction amounted to 50 - 70% in the unvegetated plots (stage 1 and 2). This may be because seedlings are quite unapparent



**Figure 16.** Average biomass ( $\pm 1$  SSE; dry weight in g) of the transplanted *Plantago maritima* individuals. Note differences in scaling between mature and juvenile plant biomass. For further explanation see Figure 13.

due to their size, or because mature plants offer a far richer harvest, and juveniles are thus neglected.

Still, competition was even more detrimental: In stage 2 and 3 (herb(-)), the biomass in competition is some 80% lower than without. When grazed, competition effects were still detectable, though less pronounced (reductions of about 60 - 80%).

Overall explained variance was quite high (70%), with age and competition contributing about 37%.

### *Plantago maritima*

Biomass increase over stage is apparent in *Plantago* seedlings (Figure 17). Like in the other three investigated species, biomass is lowest at stage 1, and differences between stages appear to exist only in the competition-free, ungrazed plots.

Herbivores removed significant amounts of *Plantago* biomass in all stages. Effects were biggest in stage 3 and juveniles suffered more than mature plants. This is due to the fact that seedlings showed a vigorous growth under optimal conditions (Figure 17, right hand side), while mature plants increased their biomass only marginally. Potential and actual take-off by hares, geese, and rabbits was therefore higher for juveniles (compare scaling in Figure!). The same argument holds true for competition: juveniles were affected stronger (a  $\times$  c \*).

Thanks to low variability of biomass within treatments, a number of interactions are significant, that in the other species were not. For *Plantago* hence some trends could be shown:

1. Herbivory affects only plants that are apparent.
2. Grazers preferred juvenile plants.
3. Seedlings were more susceptible to competition than mature plants.
4. Herbivory impacts differed between stages.

The last point might receive some further attention. As Figure 3 shows, hares and rabbits feed most in stage 1, and least in stage 3. Biomass losses due to herbivory were accordingly highest in stage 1, and least in stage 3 – but only for *Artemisia*, *Festuca* and *Halimione*. For *Plantago*, instead, the opposite was true: 85 - 95% was consumed at stage 3 (in comp(-)-plots), while only 50 - 75% in stage 1. Maybe the very palatable *Plantago* was depleted in stage 3 because it was rarely occurring. At stage 1 and 2, other palatable species like *Triglochin maritimum* reach higher abundance and *Plantago* is therefore less often used by the herbivores.

### FLOWERING

Flowering, as a measure of reproductive success, provides an additional parameter to analyse treatment effects. Plants that face abiotic conditions limiting their productivity ("stress" sensu Grime 1979), e.g. injury or resource limitations, allocate less of their production to flowers and seeds. Biomass of reproductive plant organs would have been the most sensitive variable for an analysis of treatment effects on generative reproduction. It was not measured though, due to different theoretical and practical considerations:

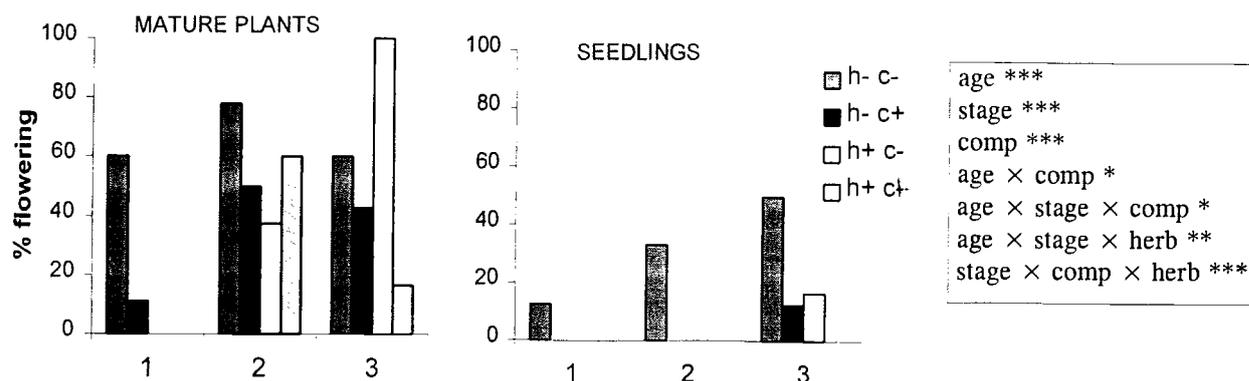


Figure 17. Flowering percentages of *Artemisia* at the three stages in the different treatments. Herbivory and competition are referred to with abbreviations.

First, herbivores might feed selectively on seeds, leading to a total loss of *Festuca* and *Plantago* flower heads by the time of harvest. Quiet often it was then practically impossible to judge whether plants flowered and were eaten or did not flower in the first place. Herbivory would thus have confounded the effects of the other factors. Second, seed set and dispersal occurred in *Festuca* and some *Plantago* plants before harvest and was therefore not measurable accurately.

Instead, flowering (and any other reproductive status) was recorded when encountered during the time when length measurements took place. Flowering rates were very different for the four species. Under natural conditions (comp(+)) and herb(+), average of all stages), 13% of the mature *Artemisia* and 40% of the *Halimione* flowered, while juvenile plants and mature *Plantago* and *Festuca* hardly ever flowered at all. Released from herbivory and competition about 50% of the mature and about 25% of the juvenile *Artemisia*, *Halimione* and *Plantago* flowered, though *Festuca* failed almost totally to show signs of reproductive development, except for one mature plant in stage 1.

### *Artemisia maritima*

The difference between mature plants and seedlings was so big that the two plant ages are

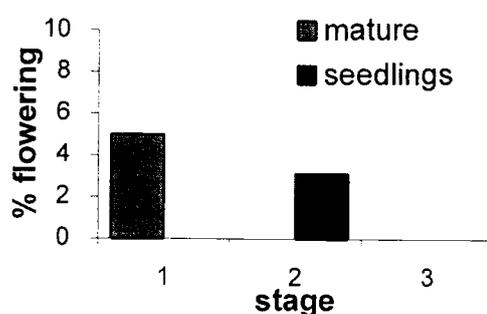
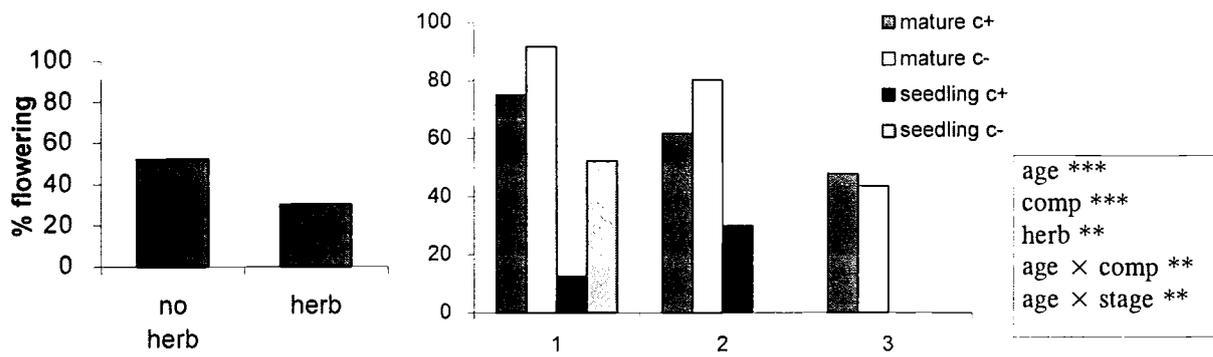


Figure 18. Flowering percentages for *Festuca rubra*. The data are to be understood as purely random despite the significance of the stage x age interaction.



**Figure 19.** Flowering percentages in *Halimione portulacoides*. Herbivory (left panel) was significant independent of the other factors. Statistic results for the interactions of plant age, stage and competition (right panel) are given in the box.

presented separately (Figure 17). In seedlings, flowering rarely occurred. Stage 3 seemed to offer the best conditions. Differences between stages and treatments were very small, however (10% represent 1 plant!).

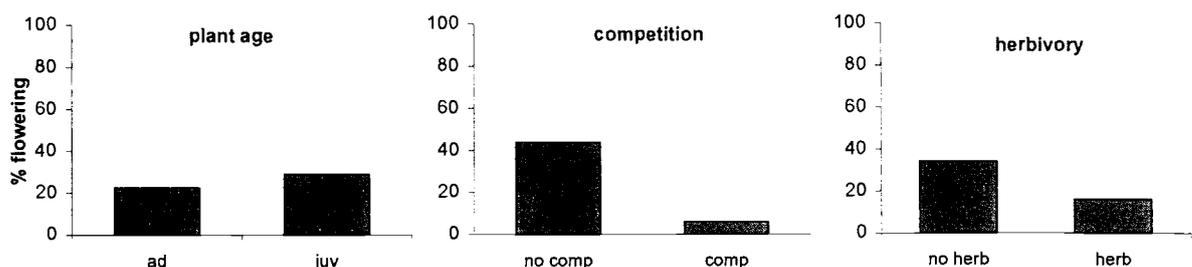
For mature plants stage caused differences in how the plants reacted to competition and herbivory. In stage 1, any of the two adversities prevented flowering, while in stage 2 and 3 both competition and herbivory were either less detrimental or could be compensated easier.

### *Festuca rubra*

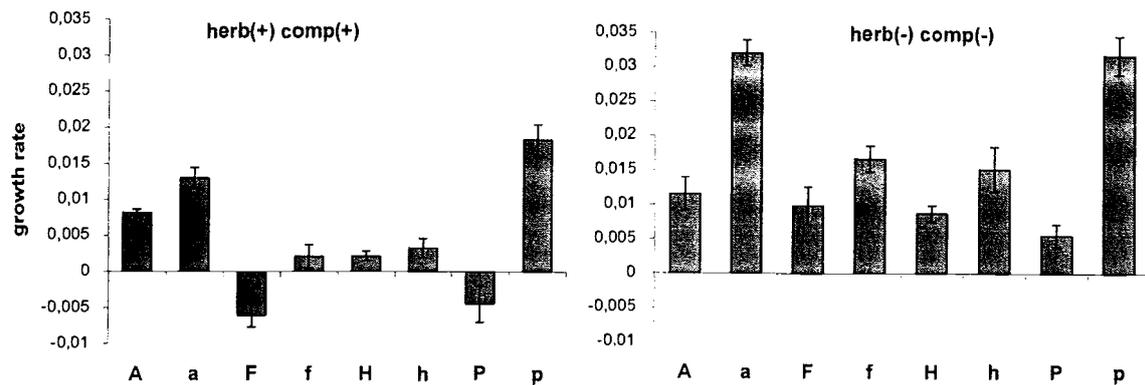
Flowering in *Festuca rubra* was a scarce event (Figure 18). The interaction of age and stage found to be significant in the logistic regression is hardly reflecting the actual importance due to the low total numbers of flowering individuals. In total, only 3 out of 240 plants produced flowers, treatment effects thus can not be detected reasonably. *Festuca* is a intensively vegetatively reproducing plant species, flowering is thus not a necessity for spreading (see *Comparison of Measured Parameters*).

### *Halimione portulacoides*

The differences between mature and juvenile plants with respect to flowering was apparent: About twice as many flowering individual were encountered in the older plant group. Here,



**Figure 20.** Flowering percentages in *Plantago maritima*. Plant age, competition, and herbivory acted independently. Stars indicate level of significance.



**Figure 21.** Growth rate  $r$  ( $\pm 1$  SSE) under natural conditions (left: herb(+) and comp(+)) and under optimal conditions (right: herb(-) and comp(-)). A growth rate of zero indicates that final weight was the same as initial. Species are referred to with the first letter of the Latin genus name, capital and small for mature and juvenile plants, respectively. For calculations see formula (7).

the effect of competition was not severe, while for the seedlings it was (Figure 19): No seedling flowered in any comp(+)-plot.

Herbivory reduced the numbers of flowering plants only marginally (Figure 19 left panel) and independently of interactions with stage, competition, or age.

### *Plantago maritima*

According to the logistic regression results, age, competition, and herbivory influenced reproductive performance significantly, though without interactions. Figure 20 shows that competition prevented flowering in 75% of the plants. Herbivory and plant age were of rather severe impact as well (65% and 25%, respectively).

## *THE DIFFERENCES BETWEEN PLANT AGES*

Juvenile plants responded stronger to the experimental manipulation than did mature plants. The weight differences in seedlings were more pronounced than in mature plants. Especially competition interacted strongly with plant age. Juveniles apparently were suppressed more by the surrounding neighbours than mature plants. Figure 21 shows that juvenile plants have a higher growth rate, thus changes in environmental conditions may result in bigger differences between treatments compared to mature plants. Under "natural" conditions, i.e.

**Table 6.** Root-to-total-weight-ratios ( $\pm 1$  SSE) for the four species. Values are calculated as root weight divided by total plant weight, average of all treatments.

species	<i>Artemisia</i>	<i>Festuca</i>	<i>Halimione</i>	<i>Plantago</i>
mature plants	0.28 (0.018)	0.66 (0.015)	0.31 (0.017)	0.63 (0.034)
seedlings	0.24 (0.012)	0.34 (0.017)	0.24 (0.018)	0.47 (0.028)

comp(+), and herb(+), mature *Festuca* and *Plantago* are not able to keep their initial weight, final biomass is hence lower than initial ( $r < 0$ ). *Halimione* and *Artemisia* transplants increased their weight only slightly. On the other hand, all juveniles showed a positive growth rate. Under "optimal" conditions, i.e. comp(-) and herb(-), all plants performed well. Still, juvenile's growth rate ( $r$ ) was in average more than twice that of mature plants.

The root-to-total-weight-ratio (RWR) of seedlings was always lower than that of mature plants (Table 7). Allocation to roots was low, for most plants had between 70 and 85% of the total biomass above-ground. In general, RWR values were rather similar within a species, which might mean, that plants begin already in the first season with an allocation strategy typical for the respective species. This pattern was neither influenced by the competition or herbivory treatments, nor by the growing conditions of the different stages. Individuals with a higher total biomass allocated more to stem and leaves ( $P < 0.001$  for all species-age-combinations except mature *Festuca*).

### Box 1: Calculation and interpretation of the relative competition and herbivory indices

The debate on the intensity of competition along productivity gradients (see *Introduction*) was shown to be partly due to the different approaches of measuring competition intensity (Grace 1995). While Grime and co-workers argued that the *absolute* reduction in performance (ACI) should be the relevant measure of competition intensity (e.g. Campbell & Grime 1992), others argued for a *relative* competition index (RCI; e.g. Wilson & Tilman 1993).

$$\text{ACI} = \text{biomass in comp(-)} - \text{biomass in comp(+)}$$

$$\text{RCI} = \frac{\text{biomass in comp(-)} - \text{biomass in comp(+)}}{\text{biomass in comp(-)}} = \frac{\text{ACI}}{\text{biomass in comp(-)}}$$

They claimed that *absolute* biomass differences would increase with absolute weight of plants (for example, due to better nutrient availability), but that still the *relative* effect of competition would be the same as in unproductive environments.

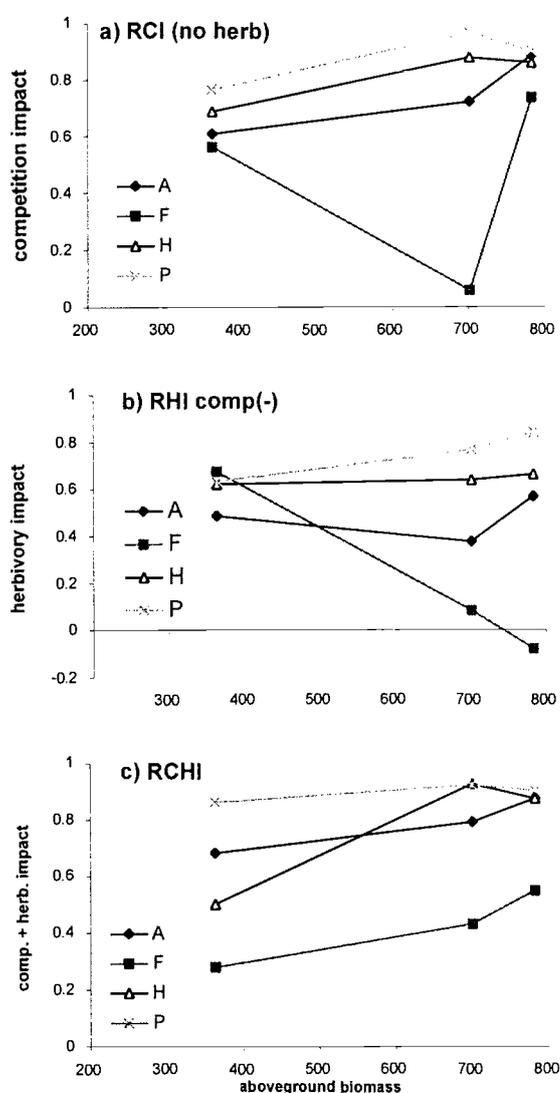
Thus, Grace (1995) suggested to give the absolute reduction values but calculate the RCI for interpretation purpose. Following this proposal, Figure 13 to 15 show the effect of competition and herbivory in terms of *absolute* biomass. For the discussion later, also relative competition and herbivory indices are calculated, with the modification of Markham & Chanway (1996). They suggested to divide by the biomass in comp(+) when this exceeds the comp(-), to let the values of CI range between -1 and 1. Their formula is given in the methods.

The interpretation of the graphs is intricate, since it is counterintuitive: The relative indices give the reduction in biomass by the factor under consideration relative to the control. Thus, increases in index values towards the maximum of 1 indicate an increase of biomass reduction due to, say, competition. Negative values, on the other hand, have to be interpreted as a better performance of the plant under the manipulation. For competition, this refers to facilitation (Bertness & Hacker 1994), while for herbivory the grazing of the neighbour plants, and thereby a reduction in the competition intensity, is the most likely way to negative values.

Seedlings had more difficulties in establishing than adults, and for *Festuca* and *Halimione* survival was lower. Also flowering occurred less often in the younger than in the older plants, which might also be a consequence of the limited ability to allocate biomass from roots and rhizomes to the flowering shoots.

### RELATIVE BIOMASS REDUCTION ALONG THE PRODUCTIVITY GRADIENT

The impact of the different treatments can be analysed using the competition and herbivory



**Figure 22.** a) Relative competition indices (RCI) of the herb(-)-plots, b) relative herbivory indices (RHI) for the comp(-)-plots and c) relative competition-herbivory-index (RCHI) for the mature plants of the four species at the three stages. Instead of stage number, biomass according to Figure 6 is plotted on the x-axis. A positive value indicates a reduction in biomass due to the respective factor: A RCI of 0.8 has to be interpreted as a 80 % reduction in biomass due to competition.

indices from formula (1) to (6). For *absolute* biomass reduction due to competition and/or herbivory, the biomass of target species are presented (Figure 13 to 16).

For *relative* biomass reduction, the RCI values for mature plants (RHI and RCHI, respectively) are given in Figure 22 (see also box 1). Seedlings indices were always very high, i.e. between 0.9 and 1, for all plant species and for both competition and herbivory. This seems to be due to the sensitivity of the seedlings: Competition and herbivory effects are of high importance for the seedling performance. For the analysis of biomass effects on plant performance these values are not taken into account, however, as they are not representative for a performance of the species, but only for the juvenile stage.

Figure 22a represents the RCI indices for mature plants: While the small growing *Plantago* experienced competition at a high level in all three stages, RCI values of *Artemisia* show a continuous increase with neighbour biomass. *Halimione* can be found somewhere in between the two. The response of *Festuca* is hardly explainable: The absence of competitive effects in stage 2 is in sharp contrast with the high values in stage 1 and 3.

The herbivory index for competition-free conditions (Figure 22b: RHI) showed a strong decrease in herbivory impact on *Festuca*, and a slightly increasing trend in the other three plants. The negative values of RHI for *Festuca* do not indicate overcompensation by the plants after being grazed, as is reported from Arctic salt marshes (Belsky 1987, Hik & Jefferies 1990). The more likely mechanism, as stated already for the negative RCI values, is that of grazing of the neighbours, resulting in a lower competition intensity.

Combining the effects of both competition and herbivory in the RCHI index, all four investigated plants show a consistent, though not significant, increase of RCHI values with stage biomass (Figure 23 c). Thus, it can be concluded that the overall *intensity* of biotic interactions only marginally increased with biomass, while the components differed between target species.

# DISCUSSION

## COMPARISON OF MEASURED PARAMETERS

Plant performance is to a certain extent influenced by nutrient availability. Especially the realisation of no-competition by removal of above-ground vegetation and trenching might have influenced the nitrogen supply by mineralization (Bertness & Shumway 1993). Trenching became common practice (e.g. Wilson & Tilman 1991, Bertness & Shumway 1993, Aarson & Epp 1990) to avoid plants in the experimental plot to be supported by plants outside, as many plants stay in below-ground contact due to vegetative spreading (Silvertown & Lovett-Doust 1994). The thereby produced dead organic matter below-ground, however, might influence microbial activity and enhance nutrient turn-over in the soil. Connell (1990) and Gadgil & Gadgil (1971) argued that trenching increases litter decomposition and nutrient release, having positive effects on the growth of the plants inside the trenched plot. On the other hand it can be argued that with the growth stop of fine roots and root hairs (low C/N-ratio), only slowly decomposing main roots and rhizomes (with high C/N-ratio) are available for the microbes, thereby trenching might also *reduce* nutrient turn-over (H. J. van Wijnen, pers. com.).

It is unclear yet which of these often overlooked processes is of major importance under which circumstances. Since they are difficult to assess, they are commonly neglected and assumed to be of minor impact on the experimental outcome. Aarson & Epp (1990) argued that the cutted vegetation should be left on the soil because nutrients which were pre-empted by the superior competitor would then be mineralised and thereby given back to the target individual. From the biomass data it is impossible to judge, if the trenching resulted in a higher nutrient supply, a lower or had no effect at all. As trenching was rarely shown to influence the outcome of experimental manipulation of competition, this method seems to be of minor importance also for the present experiment.

Survival, plant length, biomass, and flowering provide different (though interdependent) views on the performance of the target plants. Table 7 compares the results for the four species. As can be seen, results were supporting each other in most cases.

The death of a plant is the most obvious result of processes that influence its performance. On the other hand, the death of 90% of the population does not necessarily mean that it will get extinguished in the long run by the factor of interest. The other 10% might well be vigorous enough to result in a dominance of the plant species (Silvertown & Lovett Doust 1994). Transplantation definitely affected the transplanted individual. Roots were most likely damaged and individuals of *Festuca* and *Halimione* were severed from their vegetatively produced clones. Judging from the impression in the field, growth performance was not very different from the plants growing in the neighbourhood.

In a study on Mediterranean salt marshes in California, USA, Pennings & Callaway (1992) found a reduction of both survival and growth after transplanting between 25 and

70% for low salt marsh species (*Salicornia virginica* and *Arthrocnemum subterminale*). Bertness & Ellison (1987) report a decrease of biomass production of 35 to 45% and a very low survival for seedlings of *Salicornia europaea*. In how far this holds true also for the results presented here can only be speculated. Survival was indeed low, though after the second replacement a high amount of individual survived (Figure 9-12).

Plant length is a very variable parameter: Branching patterns might result in a high biomass at low total height, and leave size is very plastic as well. In this experiment, *Plantago* and *Festuca* leaves grew longer in competition while being far thinner. This can be interpreted as the plants response to the reduced light conditions near the soil surface (Figure 7). Nevertheless, length results are in good accordance with those from biomass and survival analysis.

Selective pressure on reproductive output is the driving force of evolution. Trade-offs between seed production and life expectancy, however, have led to differences in reproductive allocation (Silvertown & Lovett Doust 1994). For obligatory sexual reproducing plant species, flowering is a very good parameter to measure plant response. All of the four species investigated show some kind of vegetative reproduction, though *Artemisia* and *Plantago* are spreading mostly by means of seeds. The flowering percentages (Figure 17-20) show that the vegetative spreading *Festuca* has a far lower flowering rate than the fruit-reproducer *Artemisia* and *Plantago*. For the latter two, flowering is thus a reasonable measure of plant performance. *Halimione* produced comparatively high numbers

**Table 7.** Consistency of results: comparison of different parameters. n. s. indicates that the factor was of no explanatory value in the analysis, 'negative' and 'positive' refer to the effect of the factor on the respective parameter measured. A double hyphen means that stages of the factor were incomparable, to that results are not reasonably to interpret. Length and biomass of juveniles and adults differed initially too much to be comparable.

factor	plant species	survival	length	biomass	flowering
age	<i>Artemisia</i>	n. s.	--	--	a > j
	<i>Festuca</i>	a > j	--	--	--
	<i>Halimione</i>	n. s.	--	--	a > j
	<i>Plantago</i>	a > j	--	--	a > j
stage (productivity status)	<i>Artemisia</i>	1 = 3 > 2	2 = 3 > 1	n. s.	2 > 1 = 3
	<i>Festuca</i>	n. s.	n. s.	n. s.	--
	<i>Halimione</i>	1 = 2 > 3	2 = 3 > 1	n. s.	n. s.
	<i>Plantago</i>	1 = 3 > 2	n. s.	n. s.	n. s.
herbivory	<i>Artemisia</i>	negative	negative	negative	negative
	<i>Festuca</i>	n. s.	negative	n. s.	n. s.
	<i>Halimione</i>	negative	negative	negative	negative
	<i>Plantago</i>	negative	negative	negative	negative
competition	<i>Artemisia</i>	switch (+ to -)	positive	negative	negative
	<i>Festuca</i>	n. s.	positive	negative	n. s.
	<i>Halimione</i>	n. s.	negative	negative	negative
	<i>Plantago</i>	negative	negative	negative	negative

of flowers despite the fact that is a long-lived species and is spreading vegetatively.

### *ALLOCATION TRADE-OFFS IN THE FOUR INVESTIGATED HALOPHYTES*

All plants growing on a salt marsh have to be adapted to the constraints the regularly flooded environment poses. Salt marshes are nutrient-rich, productive systems (Gray 1992), with the exception of nitrogen (e.g. Jefferies 1977). This allows for a variety of plant strategies within the "stress-adaptation", that all species have to be labelled with (Grime 1977, 1979, Jefferies et al. 1979, Grime et al. 1988).

With reference to the four species of the present study, the following classification can be made:

1. Adaptations to salinity: *Plantago*;
2. Adaptations to herbivory: *Artemisia*, *Festuca*;
3. Adaptations to competition: *Halimione*.

Of course, these strategies are not exclusive. To simplify a plant life history to one of the three points, however, might help clarifying the basic directions of their adaptations.

In principle, evolution could have favoured species to be adapted to a wide range of salinity, as is the case for *Plantago* (Jefferies 1977, Crawford 1989). The reward is the ability to grow on a broad range of elevations and nutrient availability (Jefferies et al. 1979, Olff et al. 1997), coping easily with hypersaline conditions (Jefferies 1977). One price paid, however, might be the sensitivity of *Plantago* to herbivory and competition (see Figure 12 and 16). As most plants facing abiotic stress, *Plantago* reacts with an accumulation of stress-proteins (as proline and betaine, Crawford 1989) in the leaves, being thus attractive to herbivores (White 1984). Being a rosette plant, *Plantago* is by its morphology also susceptible to competition for light. Competition is a significant factor in all stages in the transplant biomass analysis (Figure 16), and it has the highest  $\omega^2$ -value of all four species (Figure 23). Allocating all energy to growth and physiological adaptations, *Plantago* also has the highest growth rate (Figure 21). High growth rates are predicted to lead to dominance during early stages of succession (Huston & Smith 1987, Goldberg 1990). Indeed were growth rates lower for the late-successional *Halimione*, but *Plantago* never reached dominance at the respective elevation anyhow.

The ranking of plant responses to herbivory (highest to lowest) read as: *Plantago*, *Halimione*, *Artemisia*, *Festuca*. Relative to the other species, *Artemisia* and *Festuca* apparently show adaptations to herbivory: *Artemisia* is successfully defended by the high amounts of secondary metabolic products, giving the plant its characteristic smell. *Artemisia* is nevertheless consumed, but  $\omega^2$  was as low as 2%. Geese avoid this plant species, and hares restrict their usage of it to the seedlings and the basal stem of mature plants (R. van der Wal, pers. com.), where the concentration of defence products is tasteably lower than in the upper stem and leaves (pers. observ.).

A different mechanisms can be found in *Festuca*. Like other grass species (e.g. Hik & Jefferies 1992) it allocates its resources to post-grazing re-growth rather than preventive

anti-herbivore defence. Depending on the grazing intensity this can be the superior strategy: At light grazing, re-growth investment might be less costly than the production of high amounts of complex defence-molecules in all plant tissues. At high grazing regime, however, deterring the herbivores might be a more successful approach than substituting grazed plant parts. If deterring grazers fails, as is the case with livestock grazing and *Artemisia*, the grasses with the higher re-growth allocation will be the dominant plant species (Bakker 1989, Scherfose 1993, Kiehl 1998). Apart from grazing, trampling effects play a major role at intensive livestock management, to which tap-rooted plants, as most dicotyle species, are very susceptible (Silvertown & Lovett Doust 1994).

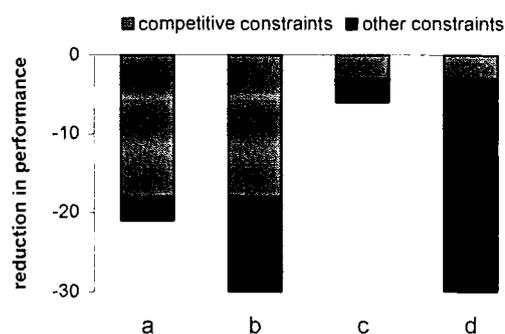
A third possible strategy, the adaptation to competition in the face of salt stress, is represented best by *Halimione*. It is a dense growing, vegetatively as well as generatively spreading shrub, which potentially dominates the low to mid salt marsh (Olf et al. 1997). Competition was the most important factor for both plant ages (with the interaction of competition and plant age only significant for *Plantago*). Effect sizes of competition were highest for *Plantago*, a little lower for *Artemisia* and *Halimione* and lowest for *Festuca* (Figure 23). Adaptations to competition thus are very likely to occur also in this extreme environment. *Halimione*'s potential to cope with anoxia and salt is a function of its nitrogen supply (Pigott 1969): Environmental stress seems to exclude it from the nutrient-poor early successional stages (Olf et al. 1997), though hare-grazing seems important for those seedlings that do establish (Drent & Van der Wal 1998). As it is not as tall a plant as, e.g., *Artemisia* or *Elymus athericus*, but nevertheless outcompetes them (Bockelmann 1997), it seems to be a decent competitor for below-ground resources. The trade-off might be *Halimione*'s vulnerability to mechanical damage, which can be ice-scouring as well as grazing. As result, trampling and grazing by livestock excludes this plant species from most of the salt marshes, restricting its occurrence to the edge of ditches and creeks (Jensen 1985, Kiehl et al. 1996, Bakker et al. 1997, Van der Wal 1998).

## THE IMPORTANCE OF COMPETITION AND HERBIVORY

### Box 2: The Intensity of Competition Versus Its Importance: An Overlooked Distinction

This is the title of an article by Welden & Slauson (1986), who were aiming to clarify the discussion about the role of competition in nature. Though few ecologists followed their suggestion and still use both words synonymously (e.g. Goldberg & Novoplansky 1997), the concept is very useful for the study presented here. It is directly transferable to herbivory as well. Definitions and modified examples in this box are taken from the original paper.

*Intensity* qualifies the *process* of competition, whereas *importance* concerns the *products* of competition. The following picture might illustrate the difference more clearly. For four different cases (a to d) the effect of competition and that of competition and other physiological constraints together are depicted in terms of reduction in performance in arbitrary units. A and b represent cases with high impact of competition and c and d such of low impact.



Competition *intensity* (= absolute effect) is the same for a and b: 18 units (c and d: 3 units). In relation to the total experiences reduction in performance, however, competition is more *important* in the cases a and c (a:  $18/21=86\%$  and c:  $3/6=50\%$  versus b:  $18/30=60\%$  and d:  $3/27=11\%$ ).

From the individual plant's point of view, competition reduces performance for 18 units (a), and the overall performance is lower than in case d, where competition only adds 3 units. Thus, competition would cause a big difference between comp(+) and comp(-)-plots in case a and b, but would contribute far more to variance of the data in case a, due to the high constraints of other factors in case b. In case c, on the other hand, competition differences would be very small, but contribution to total variance would be high, due to low other constraints. In case d, neither intensity nor importance are pronounced because of the overruling effect of the other constraints.

The two ways of presenting intensity and importance of both competition and herbivory in the discussion follow this logic: *Intensity* is calculated as the difference between plots and *importance* as effect size  $\omega^2$  (% explained variance). (That a 'relative' intensity is calculated does not turn it into an importance, because not the whole data set is used, but just the two different competition or herbivory treatments. The 'relative' only turns the arbitrary units of the example into a relative measure of performance, that is percent of optimum.)

The results of the transplantation experiment clearly show the impact of both competition and herbivory on plant biomass (Figure 13-17). Despite the fact that differences between treatment and control are sometimes very pronounced, one could argue about the *absolute* importance of competition and herbivory. That means, compared to the naturally occurring variation in plant biomass (Box 2). Other factors, such as flooding, salt or small differences in elevation also cause differences in biomass. In other words: How much of the total variation in the plant weights is explained by either competition, herbivory or their interaction?

Using formula (11), the ANOVA results of plant biomass are transferred into effect size  $\omega^2$  (% explained variance) per stage and species. The same was done for the community parameters vegetation height, plant cover, above-ground biomass, diversity, and light profiles (Table 4). The interpretation is not easy, however: A high variability of plant weights will inevitably also reduce the effect size of any experimental factor. Thus, the experimental design (as number of replicates and factors) and a low initial variance in biomass will influence the effect size substantially. The less heterogeneous seedlings grown in the greenhouse accordingly yield higher effect sizes than the nature-grown mature transplants.

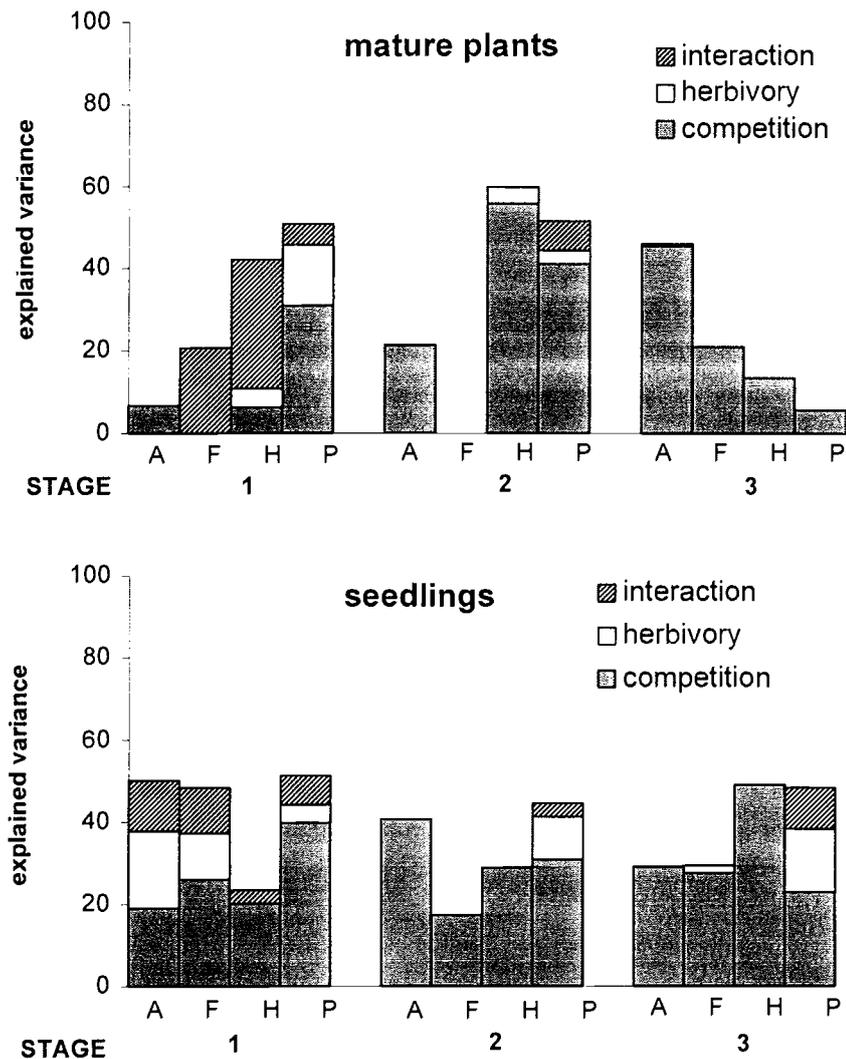
For the plant community as such, herbivory is not an important factor, given the short experimental period: Only 3% of the variance was explained by the enclosure-control difference. In stage 1, where grazing pressure by hares and rabbits was highest (Figure 8), effects were pronounced enough though, to result in significant differences in above-ground biomass (Figure 6).

In the transplanted specimen, treatments added maximally 60% variation to the weights of the target species (Figure 23). On average,  $\omega^2$ -values were as low as 28% for the mature and 38% for the seedlings. Competition on average had a higher effect size (21% and 29%, for mature and juvenile plants, respectively) than herbivory plus interaction (8% and 10%, for mature and juvenile plants, respectively). The reason to combine herbivory and interaction is that the interaction actually means that plants are grazed when they were detected, and detection is more likely to occur in the unvegetated comp(-)-plots. In that respect the detrimental effect is grazing rather than competition. Herbivory in itself was of low importance in terms of explained variance:  $\omega^2$ -values equal 2% and 5% only (mature and juvenile plants, respectively).

Particularly the mature plants of the four species differed strikingly from the average values. Herbivory is apparently most important in stage 1, while competition plays a minor role there. With increasing salt marsh age, the variance that competition added to natural variation only insignificantly increased ( $P = 0.253$ ; ANCOVA of the transformed  $\omega^2$ -values from Figure 23, species as factor, biomass as co-variable). The importance of herbivory, however, shows a significant dependency from productivity ( $P < 0.01$ ,  $F_{1,4} = 30.41$ ). Species respond significantly different to the different biomass levels (interaction of biomass and species:  $P < 0.01$ ,  $F_{3,4} = 18.01$ ). Especially in case of *Plantago* herbivory importance decreased from stage 1 to 3 (Figure 23).

These trends nicely fit the grazing intensity determined by dropping counts (Figure 3). Hares feed most intensively in stage 1, and herbivore impact is accordingly highest there. That the importance of competition does not significantly increase towards the older stages is in disagreement with the predictions of Grime (1979) and with the notion of Goldberg & Barton (1992) that higher biomass was found to result in higher competition. The only significant outcome of this analysis is the decrease of variance explained by the interaction of competition and herbivory ( $F_{1,7} = 7.06$ ,  $P < 0.05$ ), meaning probably that herbivory in stage 3 is too low to result in a significant difference between grazed and ungrazed treatments.

The apparent increase in the importance of competition for *Artemisia*, however, is contrast with the observation that it reaches higher dominance scores in stages older than 40 years (Olf et al. 1997). This trend is also recorded for *Festuca*, which only shows response to competition at stage 3 (Figure 14). The pattern of  $\omega^2$  for *Halimione* and *Plantago*, however, can not be explained except by a high initial variance in plant biomass and the unbalanced data set in case of *Plantago*.



**Figure 23.** Variance explained by competition, herbivory or their interaction for the four target species at the three stages. Upper panel refers to mature plants, lower to seedlings. Species are denoted with first letter of their Latin name.

These trends do not hold true for the seedling biomass results, though. Average values do not differ among stages ( $p > 0.2$ ), and competition is always more important than herbivory. But also here, herbivory is most pronounced in stage 1, though *Plantago* suffered biomass losses in all stages. The importance of the interaction of competition and herbivory is again decreasing with biomass ( $F_{1,7} = 12.14$ ,  $P < 0.01$ ), most likely for the same reasons mentioned for mature plants.

The total percentage explained variance is rather low. Only some 30% of the overall biomass variation can be attributed to the treatment conditions. This has to be partly attributed to the unbalanced data set with relatively few replicates. However, increasing or suppressing plant performance selectively by even less than 30% might result in pronounced vegetation changes over the years: In a five-year enclosure experiment of hares, rabbits and

geese on Schiermonnikoog, vegetation differed considerably from the surrounding vegetation (Van Wijnen et al. in prep.). The 10 % variance explained by herbivory caused this difference. Long-term consequences of grazing by geese and lagomorphs might have far greater implications than would be expected from their immediate impact (Gillham 1955, Crawley 1983, Dobson & Crawley 1994).

Commonly, published field studies do not provide enough statistical results to calculate the effects sizes of their outcome (e.g. Goldberg & Barton 1992): Of roughly 100 field studies on herbivory or competition that I encountered searching for comparable data, only four published a measure of explained variance.

In the first study, Parker & Salzman (1985) found 33% of the biomass variation of their study plant *Gutierrezia microcephala* to be explained by herbivory and additional 13% by competition. Thus their 46% are somewhat higher as the 28 to 38% found in the present study. Studying the influence of herbivory on the seedling success of a tropical tree, Sork (1987) found 28% of the variation explained by the herbivore-protection treatment. The third study is also from the salt marsh of Schiermonnikoog, dealing with *Triglochin maritimum* (Van der Wal et al. 1998). They found competition to explain 6% and herbivory 25% of the total variance; total variance explained is hence comparable to the present study. Van der Veen et al. (1998), in a study in coastal dunes, found competition to explain 60% of the variance, above-ground herbivory 3%, nematode grazing 2%, and interactions further 10% (averages of three species). Even when competition apparently is far more important in their system, herbivory impact is even smaller than in the salt marshes, ranging at the same level as the 1% of Fraser & Grime (1997). The method used to assess herbivory impact is probably one of the reasons, why grazing was not very important, as it prevented that plants in the herb(+)-plots were grazed down to the soil.

Theories differ in their predictions about the importance of herbivory along successional or productivity gradients. Oksanen et al. (1981) suggested herbivory to increase with system productivity, but when allowing herbivores to move freely along a spatial productivity gradient, their model predicted herbivory to be more important on the unproductive end of the gradient (Bonser & Reader 1995, Van de Koppel et al. 1997). In a field experiment, Reader (1992) found all mortality of target plants to be explained by herbivory, while Edwards & Gillman (1987) thought of herbivory as an unimportant factor in early successional stages. The finding of Jefferies et al. (1994) that herbivory influences vegetation development on a short-term rather than a long-term scale is probably the most reasonable conclusion from natural studies published this far.

## *THE INTENSITY OF COMPETITION AND HERBIVORY*

In contrast to importance, *intensity* refers to the difference in performance between treatment and control (Weldon & Slauson 1986; see box 2). A common way to graphically illustrate competition intensity is the relative competition index (RCI: Figure 22; see also

box 1). This index can be transferred to herbivory (Bonser & Reader 1995). The examination of Figure 23 by statistical means allows to conclude about increases of competition or herbivory intensity with site productivity: ANCOVA results are given in Table 8.

The hypothesis, that the relative competition or herbivory intensity depends on site productivity, has to be refuted by the results of the experiment presented. For both factors separately no significant increase observed, but the interaction of competition and herbivory led to a significant increase of the absolute as well as relative competition-herbivory-index. The argument that increases in survival or reproduction success will be easier to detect than trends in biomass, when the limiting resource is constantly low and not pulsed (Goldberg & Novoplansky 1997), seems not to apply to the present situation: For flowering no significant trend emerged at all, and for survival regressions of CI and HI were significant, but the slope of the regression was zero (Table 8).

How to interpret these findings? While the increasing nitrogen availability was shown to explain some successional vegetation patterns (Olf et al. 1997), *none* of the four plant species showed a significant biomass difference between stages (Table 5). This does not refute the idea of clay accretion as driving factor of succession: The surplus of nutrients is used by a higher vegetation biomass, thus resulting in maybe the same amount of nutrients available to the target species at all three stages (McGraw & Chapin 1989). The higher above-ground allocation of heavier plants can be interpreted as a consequence of competition for light at the older successional stages: Apparently, plants do not gain from below-ground investment, but from higher amounts of photosynthesising tissues. This has to be taken as an evidence that nutrients are not as much limiting as is light. As the *absolute* biomass reduction due to competition did not increase (Table 8: absolute CI), the presumably higher competition for light outleveled the gain the plants received from the higher nutrient availability. Just as herbivory prevents competition from becoming operational (Van der Wal et al. in prep.; no differences between comp(-) and comp(+)) when grazed: Figure 13-16), competition prevents the nutrient surplus to result in higher target biomass (apparent differences between stages only in the comp(-)-plots, but not in the comp(+): Figures 13-16). As the significantly increasing RCHI indicates, competition plus herbivory reduce plant biomass in all stages down to roughly the same final level: average target biomass is indifferent at the three stages at natural (= comp(+) × herb(-)) conditions (Figures 13 -16).

In an experiment in old-field plant communities, Goldberg (1987) found target biomass to decrease with neighbour biomass. Similarly, Bonser & Reader (1995) found relative intensity of competition as well as herbivory to be higher at higher neighbour biomass. They report a steep increase in the value of RCI, which levels off at about  $350 \text{ g}\cdot\text{m}^{-2}$ . This is just the value where the present study starts at. It seems that the increase in both competition and herbivory is a characteristic of very low biomass ranges.

In a review, Goldberg (1990) stated that studies addressing the question of the intensity of competition have typically found the net competition effects to be smaller (or even positive) on less productive sites. The intercontinental study of Reader et al. (1996) found

**Table 8.** ANCOVA-results of absolute and relative biomass reduction and flowering and survival<sup>1</sup> reduction due to competition and herbivory along the productivity gradient. The factor 'species' refers to the four plants, while 'regression' analysis for dependency of the data with the site biomass (the co-variable). Bold printed numbers indicate significant differences among species. Data were arcsin (square-root)-transformed prior to analysis. Back-transformed slope values (increase in index per 100 g biomass increase) are given for linear regressions that are significant or close to being so.  $N = 12$ ,  $df_{\text{species}} = 3$ ,  $df_{\text{regression}} = 1$ .

kind of index factor	absolute <sup>2</sup>					relative				
	species		regression			species		regression		
	F	p	F	p	slope	F	p	F	p	slope
CI <sub>herb(-)</sub>	0.80	0.534	0.07	0.792		2.32	0.462	0.70	0.429	
HI <sub>comp(-)</sub>	5.94	<b>0.024</b>	5.32	0.054	0.743	3.35	0.085	0.91	0.371	
CHI	6.16	<b>0.022</b>	6.80	0.035	0.816	17.09	<b>0.001</b>	14.76	0.006	0.053

kind of index factor	flowering					survival <sup>1</sup>				
	species		regression			species		regression		
	F	p	F	p	slope	F	p	F	p	slope
CI <sub>herb(-)</sub>	0.64	0.614	0.05	0.835		1.39	0.322	10.80	0.013	-0.005
HI <sub>comp(-)</sub>	0.86	0.505	0.03	0.875		0.63	0.620	9.90	0.016	0.004
CHI	0.91	0.485	0.51	0.497		5.25	<b>0.033</b>	0.57	0.474	

<sup>1</sup> Survival data from the main phase of the experiment were used, i.e. May to September.

<sup>2</sup> The values of the absolute indices are not restricted to the interval from +1 to -1 as the other indices.

*Poa pratensis* as well not to be confronted with higher competition intensity at higher biomass (with the exception of the study placed in Groningen, where the biomass range was by far highest). In an old-field experiment, Wilson & Tilman (1991) found no significant tendency for the competition intensity, despite a tendency to lower values for higher productivity. Van der Wal et al. (in prep.) provide evidence for a constant intensity of competition in a salt marsh. On average, RCI values for *Triglochin maritimum* equal 0.48, and thus were somewhat lower than for the four species presented here. Little variation in the RCI values is also reported by Van der Veen et al. (in prep.), with high average values (0.8 to 0.9) for three dune species.

As Goldberg & Novoplansky (1997) summarised, the few field studies available did not show a consistent trend, but the increase in competition intensity seemed to be restricted to the few cases, where a) the limiting resource is provided in pulses (as rain in deserts) and b) plants interact by exploitation competition during the interpulse phases. In the studied system, only condition b) seems to be realised. The limiting resource nitrogen is available, with seasonal fluctuations, throughout the year at a low supply rate (H. J. van Wijnen, pers. com.). As nitrogen supply is not strongly pulsed, the results presented are in line with the two-phase resource dynamic hypothesis of Goldberg & Novoplansky (1997), predicting competition intensity to be constant over the productivity gradient.

As Tilman (1987) pointed out, we need a better understanding of the mechanisms of competition (and herbivory as well) to produce satisfying models, which to test with

experiments. Up to now, neither models on herbivore intensity as a function of plant quality (White 1984, Coley et al. 1985) nor competition models (Grime 1979, Tilman 1988) provide a basis solid enough for the prediction of the importance and intensity of competition and herbivory along gradients of primary productivity. As well, more experiments of the type presented here are needed to establish a data set to scale models (Huston & Smith 1987, Moen & Collins 1996) and, more important, to reveal the relative importance of different mechanisms (Bengtsson et al. 1994), of which disturbances and resource fluctuations might be relevant physical agents (Connell 1975, Chesson & Huntly 1997).

### CONSEQUENCES FOR SALT-MARSH SUCCESSION

The results of the present study can be used to try understanding the process of plant species replacement during salt-marsh primary succession. One has to keep in mind that salt marshes are extreme environments, confronting plants growing there with multiple abiotic constraints such as low soil oxygen content (Howes et al. 1981), flooding (Olf et al. 1988) or nutrient limitations (Valiela & Teal 1974, Kiehl et al. 1997). It has been argued that early successional stages are accordingly too scarcely vegetated to allow plants to interact strongly (Bazzaz 1990) and that stressful habitats force the plants to trade-offs resulting in lower competition (Grime 1977). This position was challenged by Oksanen (1990) as well as by Chesson & Huntly (1997). The latter argue that in harsh environments plants might be more susceptible to competition, as their physiological state does not tolerate any more constraints. In result, biotic interactions among plants were even frequently found to act positively on plant establishment and survival, as they might provide shelter against small-scale disturbances, lessen evaporation of the soil, thus preventing salt stress to become too severe (Bertness 1991, Bertness et al. 1992, Bertness & Hacker 1994). In these cases, competition effects are overruled by beneficial effect of neighbours.

The most prominent change during the successional stages is the increase in plant cover and vegetation height (see Figure 8). If ungrazed, the mid-elevational salt marsh will inevitably develop into a uniform, dense stand of *Elymus athericus*, with both a high cover and tall canopy (Bakker 1989, Bakker et al. 1997, Van Wijnen et al. 1997). The late successional stages of the salt marsh are expected to be dominated by *Halimione portulacoides*, the only true shrub in temperate salt marshes (Chapman 1960). This seems to be the result of a good nutrient availability, however, with a clay layer of more than 15 cm (Bas Kers & Harm van Wijnen, unpubl. results). Until that stage, *Limonium vulgare* and *Puccinellia maritima* are the main plants of the lower salt marsh, while the grass *Festuca rubra* and the shrubby perennial *Artemisia maritima* dominate large parts of the mid-elevational salt marsh (Figure 1; Olf et al. 1997). It is only in the very early stages, i.e. the first 30 years, that other species as *Plantago maritima* or *Spergularia media* are common

and that plants from lower (*Salicornia spec.*, *Triglochin maritimum*) or higher elevation (*Armeria maritima*) form part of the plant community.

Increasing vegetation biomass, vegetation height and decreasing light availability (Table 4), going hand in hand with decreasing species numbers, can be suspected to result in a higher net competition intensity. The RCI values, however, do not significantly incline with biomass, and are always high for *Plantago maritima*, an early victim of succession (Table 2). What, then, is the reason for plant species replacement, if competition intensity and importance remain the same? One explanation could be that species replace each other due to passive tolerance of environmental gradients, rather than direct competition (Pickett et al. 1987): Being less sensitive to abiotic disturbance or grazing, one plant species might replace another without being competitive superior (Connell 1977). Disturbance is higher at early successional stages, however, while replacement takes place in the less disturbed, later stages (Oksanen 1990).

For an alternative explanation, the role of herbivory in succession is also worth examining. According to the theories of White (1984) and Coley (1987), early successional species are more palatable than late successional ones. They argue that disturbance is higher in the early stages, and plants thus have higher contents of stress proteins, which increase the plants quality as food (Reader & Southwood 1981, White 1984, Davidson 1993). Edwards & Gillman (1987, p. 295) stated that herbivory is a "process which influences the organisation of almost every plant community [...] rather than being an external factor". As such, herbivory is worth to be considered as a successional factor despite its low explanatory value for overall variation.

Salt-marsh plants of early stages and low elevation are indeed the preferred food species of the very selective Brent and Barnacle geese, such as *Puccinellia maritima*, *Triglochin maritimum* and *Plantago maritima* (Prop & Deerenberg 1991). Young plant parts contain high amounts of proteins, up to 35 % of the dry weight (Prop & Deerenberg 1991). Even leaf-tips of *Festuca rubra*, the main food source of hares (Snel 1994, Van der Wal 1998), still provide a protein-rich harvest for their consumers: About 20% of the dry weight is protein (Prop & Deerenberg 1991). As shown in an experiment, where hares, rabbits and geese were excluded for five years, vegetation composition might change significantly (Van Wijnen et al. 1998), in spite of the relatively low grazing pressure on the vegetation (Van der Wal 1998).

In another extreme marsh environment in the Canadian arctic, the impact of grazing and grubbing for below-ground plant parts by Lesser Snow Geese (*Chen caerulescens caerulescens*) on the development of vegetation can hardly be called other than dramatic: Some 80% of the systems primary production was consumed (Cargill & Jefferies 1984, Hik et al. 1992) and the exclusion of geese led to a dominance of species that are only scarcely present in the grazed situation (Bazely & Jefferies 1986). Nevertheless, even on this salt marsh, where herbivores might remove as little as 5% of the plant productivity (Van de Koppel et al. 1997, this thesis), it seems, that the interplay of competition and herbivory finally seems to lead to conditions that allow one species to dominate over another: RCHI values do increase during succession with site productivity (Figure 22 and Table 8). The

combined effect of competition and selective grazing reduces performance of the plant in the primary succession series even to the point of local extinction. While *Plantago maritima* finds a refuge on the high salt marsh (Olf et al. 1997), in depressions with occasionally hypersaline conditions in summer (Jefferies 1977), it (and *Triglochin maritimum* alike) can not be found at middle elevation in stages older than 50 years (pers. observ.). As well, *Halimione* seems to be excluded from early successional stages due to herbivory (Drent & Van der Wal 1998). Only on small islands in creeks which are less good accessible for hares, *Halimione* shows a vigorous growth (pers. observ.). If this has to be ascribed to the fact that it is not grazed there, or that the availability of nitrogen is higher there due to higher sedimentation, or the interaction of both factors, can only be speculated.

It is remarkable that the variation due to abiotic conditions and stochasticity (the remainder of total variation minus variation explained by competition and herbivory) does not decrease significantly with salt marsh age, i.e. nutrient availability. Chenopodes as *Halimione portulacoides*, have been found to better cope with salt stress when grown in nutrient richer soil (Pigott 1969), as has been shown for other salt-marsh species as well (Jefferies et al. 1979). Nevertheless, the influence of abiotic processes, i.e. clay sedimentation, water logging of the soil, salt stress and water shortage in summer, are at least as important as biotic interactions.

Conclusion: Even in extreme environments as on salt marshes, where plants face severe physiological constraints, biotic interactions are of critical importance. Intensities of both competition and herbivory are high, and plant species respond differently to them, depending on their life strategy. For succession, the interplay of competition and herbivory seems to play a major role. Competition showed to be most important for the performance of the target plants, but it has to be seen in the context with grazing, which does have an influence in the effects of competition. Nutrient availability, resulting in a productivity gradient in the investigated system, was of minor impact.

## ABSTRACT

Among ecologists, there is general agreement on the importance of competition and herbivory in structuring plant communities. Many field studies provide evidence for either of the two, far less, however, do so for both factors simultaneously. Hitherto, hardly any manipulation of competition as well as herbivory at sites differing in productivity were carried out. Therefore almost no empirical knowledge is available about how the importance of these two biotic interactions might change along productivity gradients. With the study presented here, experimental evidence on this topic is provided.

In a field experiment at three successional stages of a temperate salt marsh, the importance of competition and herbivory were assessed. Four plant species were transplanted as seedling and mature plants in a full-factorial design into plots with neighbours removed or present and herbivores excluded or present. Productivity as well as grazing differed among the three sites.

Competition and herbivory intensively influenced the biomass of the target species. Their relative and absolute impact did not increase significantly with site productivity. Plant species differed in their response to the biotic constraints: The palatable early-successional rosette plant *Plantago maritima* was more severely affected by both competition and herbivory than the mid-successional grass *Festuca rubra* and the late-successional shrub *Halimione portulacoides*. The mid-successional shrubby *Artemisia maritima* was only slightly less sensitive than *Plantago maritima*, despite its tall stature and unpalatable leaves.

From the results of this experiment it has to be concluded that competition as well as herbivory heavily influence plant performance and can be powerful mechanisms of vegetation succession.

## ZUSAMMENFASSUNG

### **Der Einfluß von Herbivorie, Konkurrenz und Nährstoffverfügbarkeit auf einige Pflanzen der Salzrasen.**

Für die Regelmäßigkeiten und Muster, die sich in natürlicher Vegetation finden, haben sich Konkurrenz und Herbivorie häufig als strukturierende Faktoren herausgestellt. Der Nachweis ihrer gleichzeitigen Wirkung erfolgte jedoch selten experimentell. Entsprechend besteht kein gesichertes Wissen um die relative Relevanz dieser zwei Faktoren entlang von Produktivitätsgradienten, obwohl eine reichhaltige theoretische Basis Vorhersagen hierüber macht. Mit der vorliegenden Studie soll dieser Problemkomplex angegangen werden.

Vier häufige Pflanzenarten der Salzwiese wurden in einem faktoriellen Versuchsdesign in drei Sukzessionsstadien einer Inselsalzwiese verpflanzt, jeweils als Sämling und als ausgewachsene Pflanze. In den zwei Konkurrenzmanipulationen wurden die Nachbarpflanzen oberflächlich abgeschnitten oder belassen, während für den Ausschluß der Herbivoren (Gänse, Hasen und Kaninchen) Käfige um die Versuchsflächen errichtet wurden.

Sowohl Konkurrenz als auch Herbivorie reduzierten die Biomasse der Pflanzenindividuen in signifikantem Maße. Intensität und Wichtigkeit beider biotischer Kräfte war gleich in allen drei Sukzessionsstadien. Die höhere Nährstoffverfügbarkeit in den älteren Stadien führte nicht zu einem signifikant höheren Gewicht.

Die vier Pflanzenarten unterschieden sich in ihrer Reaktion auf die Manipulationen: Die niedrigwüchsige und den Herbivoren als Futterpflanze dienende *Plantago maritima* zeigte sich am stärksten beeinflusst, während das erst später häufig werdende Gras *Festuca rubra* und der strauchige *Halimione portulacoides* weniger durch die experimentellen Behandlungen in ihrer Wuchsleistung beeinträchtigt wurden. Entgegen den Erwartungen führten sowohl Konkurrenz als auch Herbivorie zu deutlichen Effekten bei der hochwüchsigen und durch Abwehrstoffen eigentlich besser geschützte *Artemisia maritima*.

Konkurrenz und Herbivorie, so muß aus den vorliegende Ergebnissen gefolgert werden, sind wichtige Bestandteile des Sukzessionsgeschehens auf der untersuchten Inselsalzwiese, die durch eine differenzierte Beeinflussung verschiedener Pflanzenarten zu einer Veränderung der Artenzusammensetzung führen können. Zu welcher Vegetationsstruktur die beide Faktoren und ihre Interaktion mittelfristig tatsächlich führen, müssen länger andauernde Versuche zeigen.

# APPENDIX

## *TRANSPLANT-LENGTH ANALYSIS*

By measuring a growth parameter twice during the run of the experiment and at its end, it is possible to estimate whether the shift from facilitation to competition mentioned for the survival data also affects the growth of the specimen. However, this only indicates trends for above-ground performance, as length is a very plastic characteristic, dependent on the surrounding vegetation as well as abiotic disturbances (e.g. Jefferies & Rudmik 1991).

Therefore, results are only mentioned in the context of facilitation. ANOVA results and differences between treatments are presented in Table I.

In *Artemisia*, length was first lower in the unvegetated comp(-)-plots, but finally slightly higher. This holds true for the mature plants only and, overall, no effect of competition on leaf length is detectable ( $P = 0.232$ ;  $F_{1, 65} = 1.46$ ). The actual shift took place from facilitation to neutrality. Herbivory eventually influences length in *Artemisia* seedlings (but not in adults), though until early July no significant impact emerged. This pattern is inverted in *Halimione* and *Plantago*, starting with no significant difference between the two competition treatments but resulting in taller plants in the comp(-)-plots.

Mature *Festuca* plants however are facilitated by surrounding vegetation throughout the experiment. This might give a misleading impression because in the comp(-)-plots it grew denser but shorter. The phenology of the grass in the comp(+) treatment suggested a strong competition for light: leaves were thin and of a paler green than in the comp(-)-plots. Until June, *Festuca* showed no difference between stages, but finally responded to the higher nutrient availability in the latter stages. Like in *Plantago* (see below) herbivory only affected plants that are presented to the grazers on a green mesh dish: The other plants were hidden in the dense vegetation of the comp(+) treatment.

An interesting development can be seen in *Halimione*: Starting with a complex 3-way interaction (where strangely mature plants grew taller under herbivory, while seedlings did without), in July no factor shows impact and eventually, in October, all main factors are highly significant in the expected manner: Competition and herbivory led to shorter plants, and plant were taller in the older stages of the salt marsh.

*Plantago* lengths show a similar pattern. Herbivory influence disappeared in July and reappeared in the plants on the comp(-)-plots. Sheltered in the vegetation, *Plantago* seemed to be too unapparent to be significantly grazed in the comp(+)-plots.

Generally, the ANOVA outcome did confirm the expectations that mature plants grow taller than seedlings, that herbivory reduces size and that plants profit from higher nutrient levels at stage 2 and 3. As already stated, the length measurement results are valuable to detect temporal changes in significant effects because no biomass was sampled then. But their explanatory power is small due to a very variable shoot and leave morphology. For the final results, biomass measurements provide a more reliable database.

**Table 1.** Significant results of length measurements: change through time. For stage and interactions only significant levels are indicated. Because different characteristics were measured in mature *Artemisia* and seedlings, results are listed separately.

period	significant effects			difference in performance		
	1	2	3	1	2	3
<b>ARTEMISIA</b>	mature stage	stage	stage	1<2=3		
seedlings	stage	stage	stage	1<2=3	1<2=3	1<2=3
	comp	comp	herb			h+<h-
			comp	c-<c+		
<b>FESTUCA</b>		stage	stage		1<2<3	1<2=3
	comp	comp	herb			h+<h-
			comp		c-<c+	c-<c+
		stage x herb	stage x herb			h+: 1<3<2; h-: 1=2=3
		stage x comp	stage x comp			c+: 3<1<2; c-: 1<2=3
	herb x comp	herb x comp	herb x comp			h+(c-)<h-(c-)
<b>HALIMIONE</b>		stage	stage			1<2=3
		herb	herb			h+<h-
		comp	comp			c+<c-
	age		age	juv<ad	juv<ad	juv<ad
	herb x comp x age		herb x comp x age	ad: h+(c-)>h-(c-); juv: h+(c+)>h-(c+)		
		herb	herb	h+<h-		
<b>PLANTAGO</b>		stage x age	comp	juv: 1<2=3		c+<c-
		herb x comp	herb x comp			h+(c-)<h-(c-)
		herb x comp x age	herb x comp x age			h x c valid for juv. only

Abbreviations used: 1, 2, and 3 refer to stages; h- and h+ refer to the two herbivory treatments: herb(-) and herb(+), respectively; c- and c+ accordingly refer to comp(-) and comp(+); ad and juv indicate mature ("adult") plants and seedlings ("juveniles"); Combinations of symbols: h+(c-)>h-(c-) is to be read as: "In comp(-)-plots the length of plants is lower when grazed". If no further combination is given this also means, that plants did not differ in length between the two herbivory treatments in comp(+)-plots.

**Table II.** Survival rates for the different species, stages, and time periods during the run of the experiment. Data are from comp(+) $\times$  herb(+)  
treatments, thus reflecting "natural" conditions.

stage period	Artemisia mature			Artemisia juvenile			Festuca mature			Festuca juvenile			Halimione mature			Halimione juvenile			Plantago mature			Plantago juvenile		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
I	.7	1.0	.9	.8	1.0	1.0	1.0	1.0	1.0	.8	.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.7	.9	.8	.8	1.0	.9
II	.1	.2	.3	.7	.8	1.0	1.0	1.0	1.0	.1	.5	.3	.9	1.0	.5	.8	.5	.7	1.0	.9	1.0	.4	.3	.7
III	.7	.7	.7	.9	1.0	.9	1.0	1.0	1.0	.9	.6	.6	.8	1.0	.9	.8	.9	.7	.7	1.0	.8	.7	.6	.5
IV	.9	1.0	1.0	1.0	.9	.9	.9	1.0	.9	.8	.8	.8	.9	1.0	.9	.8	.7	1.0	.7	.8	.6	.9	.5	1.0
V	.8	.9	.9	1.0	.7	.6	1.0	1.0	1.0	.8	1.0	.8	1.0	1.0	1.0	.8	.8	.9	.8	.6	.8	1.0	.1	.6
mean	.64	.75	.75	.88	.89	.83	.98	.98	1.0	.74	.73	.75	.92	1.0	.86	.84	.76	.85	.78	.84	.8	.75	.48	.74

Stages are given in the second row in Arabic numbers.

Periods: I: 15.4. - 25.4.97 II: 25.4. - 13.5.97 III: 13.5. - 30.5.97 IV: 30.5. - 4.7.97 V: 4.7. - 1.10.97T

## REFERENCES

- Aarssen, L.W. & G.A. Epp (1990) Neighbour manipulations in natural vegetation: a review. *J. Veg. Sci.* **1**: 13-30.
- Angerbjörn, A. (1983) Reliability of pellet density estimates of Mountain Hares. *Finish Game Res.* **41**: 15-20.
- Bakker, J.P. (1989) Nature Management by Grazing and Cutting. Kluwer Academic, Dordrecht.
- Bakker, J.P., P. Esselink, R. Van Der Wal & K.S. Dijkema (1997) Options for restoration and management of coastal salt marshes in Europe. Pp. 267-297 in: Restoration Ecology And Sustainable Development (Eds. K.M. Urbanska, N.R. Webb & P.J. Edwards). Cambridge University Press, Cambridge.
- Bazely, D.R. & R.L. Jefferies (1986) Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. *J. Ecol.* **74**: 693-706.
- Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Ann. Rev. Ecol. Syst.* **10**: 351-371.
- Bazzaz, F.A. (1990) Plant-plant interactions in successional environments. Pp. 239-263 in: Perspectives in Plant Competition (Eds. J.B. Grace & D. Tilman). Academic Press, New York.
- Begon, M., J.L. Harper & C.R. Townsend (1990) Ecology. Blackwell, Cambridge.
- Belsky, A.J. (1987) The effect of grazing: confounding of ecosystem, community, and organism scale. *Am. Nat.* **129**: 777-783.
- Bengtsson, J., T. Fagerström & H. Rydin (1994) Competition and coexistence in plant communities. *Tren. Ecol. Evol.* **9**: 246-250.
- Bertness, M.D. (1991) Interspecific interactions among high marsh perennials in a New England (USA) salt marsh. *Ecology* **72**: 125-137.
- Bertness, M.D. & A.M. Ellison (1987) Determinants of pattern in a New England salt marsh plant community. *Ecol. Mono.* **57**: 129-147.
- Bertness, M.D., L. Gough & S.W. Shumway (1992) Salt tolerance and the distribution of fugitive salt marsh plants. *Ecology* **73**: 1842-1851.
- Bertness, M.D. & S.D. Hacker (1994) Physical stress and positive associations among marsh plants. *Am. Nat.* **144**: 363-372.
- Bertness, M.D. & S.W. Shumway (1993) Competition and facilitation in marsh plants. *Am. Nat.* **142**: 718-724.
- Bestmann, M. & R. Keizer (1996) Draagkracht van de Oosterkwelder van Schiermonnikoog voor de haas (*Lepus europaeus* Pallas). Master's Thesis, Univ. Wageningen, the Netherlands.
- Bockelmann, A.C. (1996) Das Ausbreitungspotential von *Elymus x oliveri* - Analyse eines experimentell-ökologischen Versuchsansatzes. Master's Thesis, Uni. Kiel, Germany.
- Bonser, S.P. & R.J. Reader (1995) Plant competition and herbivory in relation to vegetation biomass. *Ecology* **76**: 2176-2183.
- Campbell, B.D. & J.P. Grime (1992) An experimental test of plant strategy theory. *Ecology* **73**: 15-29.
- Cargill, S.M. & R.L. Jefferies (1984) The effects of grazing by Lesser Snow Geese on the vegetation of a sub-arctic salt marsh. *J. Appl. Ecol.* **21**: 669-686.
- Chapman, V.J. (1960) Salt Marshes and Salt Deserts of the World. Interscience, New York.
- Chesson, P. & N. Huntly (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am. Nat.* **150**: 519-553.
- Coley, P.D. (1987) Interspecific variation in plant anti-herbivore properties: the role of habitat quality and rate of disturbance. *New Phytologist* **106** (Supplement): 251-263.
- Connell, J.H. (1975) Some mechanisms producing structure in natural communities. Pp. 460-490 in: Ecology and Evolution of Communities (Eds. M.L. Cody & J.M. Diamond). Harvard Uni. Press, Cambridge.

- Connell, J.H. (1977) Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302-1310.
- Connell, J.H. (1990) Apparent versus "real" competition in plants. Pp. 9-27 *in*: Perspectives in Plant Competition (Eds. J.B. Grace & D. Tilman).
- Connell, J.H. & R.O. Slayter (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* **111**: 1119-1144.
- Cooper, W.S. (1923) The recent ecological history of Glacier Bay, Alaska. III. Permanent quadrats at Glacier Bay: An initial report upon a long-period study. *Ecology* **4**: 355-365.
- Cooper, W.S. (1939) A fourth expedition to Glacier Bay, Alaska. *Ecology* **20**: 130-159.
- Cowles, H.C. (1899) The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Botanical Gazette* **27**: 95-391.
- Crawford, R.M.M. (1989) Studies in Plant Survival. Blackwell, Oxford.
- Crawley, M.J. (1983) Herbivory. The Dynamics of Animal-Plant Interactions. Blackwell, Oxford.
- Crawley, M.J. (1993) GLIM for Ecologists. Blackwell, Oxford.
- Crawley, M.J. (1997) Plant-herbivore interactions. Pp. 401-474 *in*: Plant Ecology (Ed. M.J. Crawley). 2nd edition, Blackwell, Oxford.
- Davidson, D.W. (1993) The effects of herbivory and granivory on terrestrial plant succession. *Oikos* **68**: 23-35.
- De Leeuw, J., W.D.H. Olf & J.P. Bakker (1993) Does zonation reflect the succession of salt-marsh vegetation? A comparison of an estuarine and a coastal bar island marsh in the Netherlands. *Acta Bot. Neerl.* **42**: 435-445.
- Diamond, J.M. (1986) Overview: Laboratory experiments, field experiments, and natural experiments. Pp. 3-22 *in*: Community Ecology (Eds. J.M. Diamond & T.J. Case). Harper & Row, New York.
- Diamond, J.M. & T.J. Case (1986) Introduction. Pp. 4-6 *in*: Community Ecology (Eds. J.M. Diamond & T.J. Case). Harper & Row, New York.
- Dobson, A.P. & M.J. Crawley (1994) Pathogens and the structure of plant communities. *Tren. Ecol. Evol.* **9**: 393-398.
- Drent, R.H. & R. van der Wal (1998) Cyclic grazing in vertebrates and the manipulation of the food resources. *in*: Plants, Herbivores, and Predators (Eds. H. Olf, V.K. Brown & R.H. Drent). Blackwell, Cambridge.
- Edwards, P.J. & M.P. Gillman (1987) Herbivores and plant succession. Pp. 295-314 *in*: Colonization, Succession and Stability (Eds. A.J. Gray, M.J. Crawley & P.J. Edwards). Blackwell Scientific Publ. Oxford.
- Ellison, A.M. (1987) Effects of competition, disturbance, and herbivory on *Salicornia europaea*. *Ecology* **3**: 576-586.
- Gadgil, R.L. & P.D. Gadgil (1971) Mycorrhiza and litter decomposition. *Nature* **233**: 133
- Gaudet, C.L. & P.A. Keddy (1988) A comparative approach to predicting competitive ability from plant traits. *Nature* **334**: 242-243.
- Gerlach, A., E.A. Albers & W. Broedlin (1994) Development of the nitrogen cycle in the soils of a coastal dune succession. *Acta Bot. Neerl.* **43**: 189-203.
- Gillham, M.E. (1955) Ecology of the Pembrokeshire Islands. III. The effect of grazing on the vegetation. *J. Ecol.* **43**: 172-206.
- Glenn-Lewin, D., C & E. van der Maarel (1992) Patterns and processes of vegetation dynamics. Pp. 11-59 *in*: Plant Succession (Eds. D.C. Glenn-Lewin, K. Peet & T.T. Veblen). Chapman & Hall, London.
- Goldberg, D.E. (1987) Neighborhood competition in an old-field plant community. *Ecology* **68**: 1211-1223.
- Goldberg, D.E. (1990) Components of resource competition in plant communities. Pp. 27-49 *in*: Perspectives on Plant Competition (Eds. J.B. Grace & D. Tilman). Academic Press, New York.

- Goldberg, D.E. & A.M. Barton (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am. Nat.* **139**: 771-801.
- Goldberg, D.E. & L. Fleetwood (1987) Competitive effect and response in four annual plants. *J. Ecol.* **75**: 1131-1143.
- Goldberg, D.E. & A. Novoplansky (1997) On the relative importance of competition in unproductive environments. *J. Ecol.* **85**: 409-418.
- Grace, J.B. (1990) On the relationship between plant traits and competitive ability. Pp. 51-65 in: *Perspectives on Plant Competition* (Eds. J.B. Grace & D. Tilman). Academic Press, New York.
- Grace, J.B. (1995) On the measurement of plant competition intensity. *Ecology* **76**: 305-308.
- Gray, A.J. (1992) Saltmarsh plant ecology: zonation and succession revisited. Pp. 63-79 in: *Saltmarshes. Morphodynamics, Conservation & Engineering Significance* (Eds. J.R.I. Allen & K. Pye). Cambridge Uni. Press, Cambridge.
- Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature* **242**: 344-347.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance for ecological and evolutionary theory. *Am. Nat.* **111**: 1169-1194.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley, Chichester.
- Grime, J.P., J.G. Hodgson & R. Hunt (1988) *Comparative Plant Ecology*. Hyman, London.
- Gurevitch, J. & S.L. Collins (1994) Experimental manipulation of natural plant communities. *Tren. Ecol. Evol.* **9**: 94-98.
- Hays, W.L. (1981) *Statistics*. Holt, Rinehart, & Winston, New York.
- Hik, D.S. & R.L. Jefferies (1990) Increases in the net above-ground primary production of a salt-marsh forage grass: A test of the predictions of the herbivore-optimization model. *J. Ecol.* **78**: 180-195.
- Hik, D.S., R.L. Jefferies & A.R.E. Sinclair (1992) Foraging by geese, isostatic uplift and asymmetry in the development of salt-marsh plant communities. *J. Ecol.* **80**: 395-406.
- Howes, B.L., R.W. Howarth, J.M. Teal & I. Valiela (1981) Oxidation-reduction potentials in salt marshes: spatial patterns and interactions with primary productivity. *Limnology and Oceanography* **26**: 350-360.
- Huisman J, Olff H & Fresco LFM (1993) A hierarchical set of models for species response analysis. *J. Veg. Sci.* **4**: 37-46.
- Huisman, J., J.P. Grover, R. Van Der Wal & J. Van Andel (1997) Competition for light, plant species replacement, and herbivory along productivity gradients. Pp. 159-182 in: *The Struggle For Light* (Ed. J. Huisman). PhD-thesis Univ. Groningen.
- Huston, M. & T. Smith (1987) Plant succession: life history and competition. *Am. Nat.* **130**: 168-198.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia or Why are there so many kinds of animals? *Am. Nat.* **93**: 145-158.
- Jefferies, R.L. (1977) Growth response of coastal halophytes to inorganic nitrogen. *J. Ecol.* **65**: 847-865.
- Jefferies, R.L., A.J. Davy & T. Rudmik (1979) The growth strategies of coastal halophytes. Pp. 243-268 in: *Ecological Processes in Coastal Environments* (Eds. R.L. Jefferies, A.J. Davy & T. Rudmik). Rep. 26th BES Conf. London.
- Jefferies, R.L., D.R. Klein & G.R. Shaver (1994) Vertebrate herbivores and northern plant communities: reciprocal influences and responses. *Oikos* **71**: 193-206.
- Jefferies, R.L. & T. Rudmik (1991) Growth, reproduction and resource allocation in halophytes. *Aquat. Bot.* **39**: 3-16.
- Jensen, A. (1985) The effect of cattle and sheep grazing on salt-marsh vegetation at Skallingen, Denmark. *Vegetatio* **60**: 37-48.
- Keddy, P.A. (1989) *Competition*. Chapman & Hall, London.

- Kers, A.S., S.R. Van der Brug, D. Bos & J.P. Bakker (1998) Vegetatiekartering Oost-Schiermonnikoog, 1993-1996. Groningen.
- Kiehl, K. (1998) Vegetationsmuster in Vorlandsalzwiesen in Abhängigkeit von Beweidung und abiotischen Standortfaktoren. *Mitteilungen der AG Geobotanik SH und HH* **52**: 1-142.
- Kiehl, K., I. Eischeid, S. Gettner & J. Walter (1996) Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. *J. Veg. Sci.* **7**: 99-106.
- Kiehl, K., P. Esselink & J.P. Bakker (1997) Nutrient limitation and plant species composition in temperate salt marshes. *Oecologia* **111**: 325-330.
- Krebs, C.J. (1989) *Ecological Methodology*. Harper Collins, New York.
- Londo, G. (1976) The decimal scale for relevés of permanent quadrats. *Vegetatio* **33**: 61-64.
- Louda, S.M., K.H. Keeler & R.D. Holt (1990) Herbivore influences on plant competitive interactions. Pp. 413-444 in: *Perspectives on Plant Competition* (Eds. J.B. Grace & D. Tilman). Academic Press, London.
- Markham, J.H. & C.P. Chanway (1996) Measuring plant neighbour effects. *Funct. Ecol.* **10**: 548-549.
- McAuliffe, J.R. (1986) Herbivore-limited establishment of a Sonoran desert tree. *Ecology* **67**: 276-280.
- McGraw, J.B. & F.S. Chapin, III (1989) Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology* **70**: 736-749.
- Menard, S. (1995) *Applied Logistic Regression Analysis*. Nr. 106. SAGE Uni. Paper, London.
- Menge, B.A. (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecol. Mono.* **65**: 21-74.
- Menge, B.A. & T.M. Farrell (1987) Community structure and interaction webs in shallow marine hard-bottom communities: tests of an environmental stress model. *Adv. Ecol. Res.* **19**: 189-259.
- Moen, J. & S.L. Collins (1996) Trophic interactions and plant species richness along a productivity gradient. *Oikos* **76**: 603-607.
- Newman, E.I. (1973) Competition and diversity in herbaceous vegetation. *Nature* **244**: 310
- Noble, I.R. & R.O. Slayter (1980) The use of vital attributes to predict successional change in plant communities subject to recurrent disturbances. *Vegetatio* **43**: 5-21.
- Oksanen, L. (1990) Predation, herbivory, and plant strategies along gradients of primary productivity. Pp. 445-474 in: *Perspectives in Plant Competition* (Eds. J.B. Grace & D. Tilman). Academic Press, London.
- Oksanen, L., S.D. Fretwell, J. Arruda & P. Niemelä (1981) Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 240-261.
- Olf, H., J.P. Bakker & L.F.M. Fresco (1988) The effect of fluctuations in tidal inundation frequency on a salt-marsh vegetation. *Vegetatio* **78**: 13-19.
- Olf, H., J. De Leeuw, J.P. Bakker, R.J. Platerink, H.J. Van Wijnen & W. De Munck (1997) Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. *J. Ecol.* **85**: 799-814.
- Olf, H., J. Huisman & B.F. Van Tooren (1993) Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. *J. Ecol.* **81**: 693-706.
- Olson, J.S. (1958) Rates of succession and soil change on southern Lake Michigan sand dunes. *Botanical Gazette* **119**: 125-170.
- Parker, M.A. & A.G. Salzman (1985) Herbivore exclusion and competitor removal: effects on juvenile survivorship and growth in the shrub *Gutierrezia microcephala*. *J. Ecol.* **73**: 903-913.
- Pennings, S.C. & R.M. Callaway (1992) Salt marsh plant zonation: The relative importance of competition and physical factors. *Ecology* **73**: 681-690.
- Pickett, S.T.A. (1987) Space-for-time substitution as an alternative to long-term-studies. Pp. 110-135 in: *Long-Term Studies in Ecology - Approaches and Alternatives* (Ed. E. Likens). Springer, New York.

- Pickett, S.T.A., S.L. Collins & J.J. Armesto (1987) Models, mechanisms and pathways of succession. *Bot. Rev.* **53**: 335-371.
- Prop & Deerenberg (1991) Spring staging in brent geese *Branta bernicla* : Feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* **87**: 19-28.
- Reader, R.J. (1992) Herbivory as a confounding factor in an experiment measuring competition among plants. *Ecology* **73**: 373-374.
- Reader, R.J. & T.R.E. Southwood (1981) The relationship between palatability to invertebrates and the successional status of a plant. *Oecologia* **51**: 271-275.
- Reader, R.J., S.D. Wilson, J.W. Belcher, I. Wisheu, P.A. Keddy, D. Tilman, E.C. Morris, J.B. Grace, H. Olf, R. Turkington, E. Klein, Y. Leung, B. Shipley, R. Van Hulst, M.E. Johansson, C. Nilsson, J. Gurevitch, K. Grigulis & B.E. Beisner (1994) Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. *Ecology* **75**: 1753-1760.
- Rice, K.J. (1987) Interaction of disturbance patch size and herbivory in *Erodium* colonization. *Ecology* **68**: 1113-1115.
- Roozen, A.J.M. & V. Westhoff (1985) A study on long-term salt marsh succession using permanent plots. *Vegetatio* **61**: 23-32.
- Scherfose, V. (1993) Zum Einfluß der Beweidung auf das Gefäßpflanzen-Artengefüge von Salz- und Brackmarschen. *Zeitschrift für Ökologie und Naturschutz* **2**: 201-211.
- Silvertown, J.W. & J. Lovett Doust (1994) Introduction to Plant Population Biology. Blackwell, Oxford.
- Snel, J. (1994) Dieetkeuze van hazen (*Lepus europaeus* Pallas) en konijnen (*Oryctolagus cuniculus* L.) op de Oosterkwelder van Schiermonnikoog: en vergelijking. Master's Thesis, Univ. Wageningen, the Netherlands.
- Sokal, R.R. & F.J. Rohlf (1995) Biometry. Freeman, New York.
- Sork, V.L. (1987) Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecology* **68**: 1341-1350.
- Tilman, D. (1985) The resource-ratio hypothesis of plant succession. *Am. Nat.* **125**: 827-852.
- Tilman, D. (1986) Evolution and differentiation in terrestrial plant communities: the importance of the soil resource:light gradient. Pp. 359-380 in: Community Ecology (Eds. J.M. Diamond & T.J. Case). Harper & Row, New York.
- Tilman, D. (1987) The importance of the mechanisms of interspecific competition. *Am. Nat.* **129**: 768-774.
- Tilman, D. (1988) Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton, New Jersey.
- Tilman, D. & D. Wedin (1991) Dynamics of nitrogen competition between successional grasses. *Ecology* **72**: 1038-1049.
- Timmerman, E. & J. Wolff (1997) Het terreingebruik en de dieetkeuze van hazen (*Lepus europaeus* Pallas) op de Oosterkwelder van Schiermonnikoog. Report Zoological Laboratory, Univ. Groningen, the Netherlands.
- Valiela, I. & J.M. Teal (1974) Nutrient limitation in salt marsh vegetation. Pp. 547-563 in: Ecology of Halophytes (Eds. R.J. Reimold & W.H. Queen). Academic Press, New York.
- Van de Koppel, J. (1997) Trophic Interactions in Gradients of Primary Productivity. PhD-thesis, University Groningen.
- Van de Koppel, J., J.M. Fryxell & R. Van Der Wal (1997) Consequences of herbivore mobility for exploitation in patchy ecosystems. Pp. 47-65 in: Trophic Interactions in Gradients of Primary Productivity (Ed. J. Van de Koppel). Ph.D. - Thesis, Univ. Groningen.
- Van de Koppel, J., J. Huisman, R. van der Wal & H. Olf (1996) Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology* **77**: 736-745.

- Van der Veen, A., C. Kaldewey & J.P. Bakker (in prep.) Above- and below-ground herbivory affect plant competition along a successional gradient of dry coastal sand dunes. Submitted to *J. Ecol.*
- Van der Wal, R. (1998) Defending the Marsh – Herbivores in a Dynamic Coastal Ecosystem. Ph.D. - Thesis, Univ. of Groningen, the Netherlands.
- Van der Wal, R., M. Egas, A. Van der Veen & J.P. Bakker (in prep.) Effects of herbivory and competition on growth and reproduction of *Triglochin maritima* in a gradient of primary productivity. Submitted to *Ecology*.
- Van Wijnen, H.J. & J.P. Bakker (1997) Nitrogen accumulation and plant species replacement in three salt marsh systems in the Wadden Sea. *J. Coast. Conserv.* 3: 19-26.
- Van Wijnen, H.J., J.P. Bakker & Y. De Vries (1997) Twenty years of salt-marsh succession on the coastal barrier island of Schiermonnikoog (The Netherlands). *J. Coast. Conserv.* 3:
- Van Wijnen, H.J., R. Van Der Wal & J.P. Bakker (in prep.) The impact of small herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. submitted to *Oecologia*.
- Weldon, C.W. & W.L. Slauson (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. *Quart. Rev. Biol.* 61: 23-44.
- White, T.C.R. (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63: 90-105.
- Wilson, S.D. & D. Tilman (1991) Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72: 1050-1065.
- Wilson, S.D. & D. Tilman (1993) Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74: 599-611.
- Zentralstelle für die floristische Kartierung der BRD (1997) Standardflorenliste der Farn- und Blütenpflanzen der Bundesrepublik Deutschland. *Flor. Rundbr. Beih.* 3: 1-470.

# SALT-MARSH NEMATODES DO NOT LIVE UP TO THEIR REPUTATION AS REGULATORS OF PLANT PERFORMANCE<sup>1</sup>

*Abstract* - In an experiment, we tested whether the removal of nematodes by means of nematicide application would enhance plant performance or influence plant competition. The study was conducted in a temperate salt marsh, involving the two common plant species *Artemisia maritima* and *Festuca rubra* growing on intact sods collected from the field. Half of the sods were treated with 'Nemacure', a nematicide controlling both endo- and ectoparasitic nematodes. In untreated soil, the number of both total and plant-parasitic nematodes were high, relative to other systems. Despite the efficacy of the nematicide, by which about 90% of the nematodes were eliminated, no effects on plant biomass nor competitive ability of the two plant species were found

## INTRODUCTION

The impact of below-ground herbivores on plant species dynamics is poorly understood (Brown 1990, Mortimer et al. 1998). Most studies on herbivory focus on above-ground grazing, although the impact of below-ground herbivores might be much greater (Weaver and Smolik 1987). Plants allocate about 60 to 90% of the primary production to below-ground parts (Stanton 1988), available to vast number of soil-dwelling herbivores throughout the year.

Nematodes are the most abundant multicellular soil organisms (Peterson 1982a). The impact of nematodes on below-ground processes is diverse. Nematodes can have a profound effect on nutrient cycling by feeding on bacteria (Ingham et al. 1986ab, Stanton et al. 1981). Moreover, by grazing on arbuscular mycorrhizal fungi (AMF), nematodes may reduce plant growth (Ingham et al. 1986b). Plant-feeding nematodes can affect plant performance also directly (Van der Putten et al. 1993, Van der Putten & Van der Stoel 1998). In grassland ecosystems, where nematodes may consume as much as 60% of the

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total primary production (Andrzejewska & Gyllenberg 1980, Smolik 1977), nematodes have to be considered the major herbivore (Stanton 1988).

Plant-feeding nematodes might influence the competitive balance between plant species (Gates et al. 1986, Price et al. 1986, Van der Putten & Peters 1997). These effects were observed in studies on crop-weed interactions (Pantone 1995, Powers et al. 1994), but in other studies, no such effects were found (Chen et al. 1995, Ponce et al. 1995). The impact of phytophagous nematodes on plant competition has rarely been studied in natural plant communities (Griffin 1984, Stanton 1988). An exception is formed by studies in dune systems (Van der Putten & Peters 1997, De Rooij-Van der Goes 1995, Van der Veen et al. in prep) and semi-arid grassland (Stanton et al. 1981, Ingham et al. 1986ab).

On the basis of a series of pot experiments performed under greenhouse conditions, Van der Putten and colleagues showed that soil-born diseases (plant-parasitic nematodes and pathogenic fungi) could play an important role in coastal foredune succession (Van der Putten et al. 1993, Van der Putten and Peters 1997, Van der Putten and Van der Stoel 1998). There, *Ammophila arenaria* (L.) Link is followed in sequence by *Festuca rubra* L. and *Carex arenaria* L. with *Elymus athericus* L.. Biomass production in seedlings of all four plant species depended strongly on the origin of the rhizosphere soil. When soils were sterilised by gamma radiation, in order to wipe out micro-organisms, no difference were found anymore. *Festuca rubra* showed a gradual decrease in biomass production along a series of unsterilised soils originating from *Ammophila arenaria* to *Elymus athericus*, i.e. plants dominating earlier versus later in succession (Van der Putten et al. 1993).

In the present study, we investigated the effects of nematodes on plant performance and plant competition in a natural salt-marsh system. Based on the findings of Van der Putten and co-workers we expected nematodes to influence plant performance in the higher parts of salt marsh, which are also dominated by *Festuca rubra* and *Elymus athericus* (Olf et al. 1997). Lower on the salt marsh, above-ground grazing by small herbivores such as geese and hares was shown to strongly affect the rate of successional change (Drent & Van der Wal 1998), plant species abundance (Van Wijnen et al. in prep.), and modify competitive interactions among plants (Van der Wal et al. in prep). The impact of below-ground herbivores on vegetation processes, however, remained unclear.

We hypothesise that root-feeding nematodes will influence plant growth and competitive interactions among plant species. To test this hypothesis, we manipulated nematode abundance in sods dominated by *Artemisia maritima* L., *Festuca rubra*, and mixtures of both. These plant species are characteristic of mid elevational parts of temperate European salt marshes (Westhoff & Den Held 1969).

## METHODS

### *SITE DESCRIPTION*

The study was conducted on the island of Schiermonnikoog, the Netherlands. Sods were collected in a 40-year-old salt marsh at about 45 cm above mean high tide, grazed by geese and hares. Here, *Artemisia* and *Festuca* together account for about 90% of total plant cover. Both plant species grow in mixed and single-species stands, creating a fine-grained vegetation pattern. In the study area, *Artemisia* and *Festuca* co-occur during vegetation succession, but will be inevitably replaced by *Elymus athericus* in older marshes (Bakker et al. 1997). For a detailed description of the vegetation see Olf et al. (1997).

### *SAMPLING AND SET-UP*

On 20 June 1997, sods of 12 cm  $\varnothing$  and 12 cm depth were cut out of pure and mixed stands of *Artemisia* and *Festuca*, and were placed in similar sized plastic pots. Other species occurring in the pots were picked out manually. Half of the pots were randomly assigned as controls, whereas the other half was treated with the slow-release nematicide 'Nemacure' (10 % Fenamiphos, Bayer AG, Germany), applied at the highest suggested dose of 20 g/m<sup>2</sup>. To avoid negative impact on green plant parts, granules were pressed into the clayey soil surface. Nemacure controls ectoparasites, endoparasites, free-living, cyst-forming and root-knot nematodes, but has no effect on bacteria.

Each pot was assigned to one of three categories, i.e. *Artemisia* monoculture, *Festuca* monoculture, or mixed stand of the two species, and was either subject to the nematicide treatment or served as a control. For monocultures, we used 10 replicates per treatment, whereas 16 replicates were used for the mixed stands. Labelled pots were placed randomly on a table outside the field station in complete sunlight. Plants were watered during periods of drought. Transfer of nematodes via leaking water was prevented using dishes under every single pot. Pots were widely spaced to avoid direct contact or shading effects.

The experiment lasted for nearly four months, from 22 June to 10 October 1997. We used biomass as a measure of plant performance. For this, contents of all pots were washed over a sieve. The plant material was separated into above- and below-ground parts, dried at 70°C for 48 hours, and weighted. Initial plant biomass was determined at the start of the experiment in 5 randomly selected additional sods of both monocultures and mixture. Soil samples were taken (N=3 per treatment) to determine nematode abundance and species composition.

### *DETERMINATION OF NEMATODES*

For extraction of nematodes, we followed the protocol of Southey (1986). Hundred g of fresh soil per pot was rinsed into an Oostenbrink III elutriator with a constant water pressure of 1 l/min. Nematodes in the water column were washed over 4 sieves (0.045 mm mesh size), collected in a plastic bowl and poured through a double-layer sandwich-filter made of cotton wool. The filters were kept overnight at 20°C in contact to water, allowing nematodes to crawl through the filter layer into the water. Nematodes were aggregated in a vial, which was filled to 100 ml with tap water and mixed thoroughly. Three subsamples of 2 or 5 ml (untreated and nematicide treated, respectively) were inspected and counted under a stereoscope (32 ×). Per sample, about hundred randomly selected nematodes were determined to genus level. The ratio of the abundance of the different genera were used to convert total number of counted nematodes into number per genus.

### *INDICES AND STATISTICS*

To compare the relative importance of nematode herbivory and plant competition on the biomass ratio of *Artemisia* and *Festuca*, two indices were calculated according to Bonser and Reader (1995), by using average values for each treatment. Relative nematode influence (RNI) was calculated as:

$$\text{RNI} = \frac{\text{final biomass in treated pots} - \text{final biomass in control pots}}{\text{final biomass in treated pots}}$$

The relative influence of interspecific competition (RCI) in analogy is given by:

$$\text{RCI} = \frac{\text{final biomass in monoculture} - (\text{final biomass in mixture}) \cdot C}{\text{final biomass in monoculture}}$$

where C = initial biomass in monoculture divided by the initial biomass in mixture.

Analysis of main effects employed Analysis of Variance (ANOVA); post-hoc comparisons were carried out using Tukey's honestly significant difference test (Tukey's hsd) for plant biomass, and least significant difference contrast (LSD) for nematode numbers. Transformed data met ANOVA assumptions of homoscedasticity and normal distribution.

# RESULTS

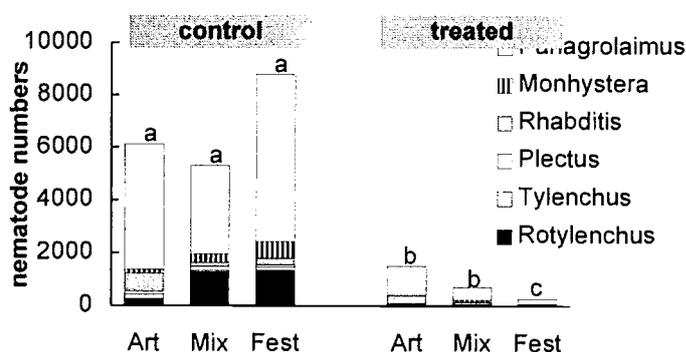
## NEMATOCIDE APPLICATION

Total number of nematodes were strongly reduced by nematicide application ( $F_{1, 15} = 46.8$ ,  $P < 0.001$ ; Figure 1). Reductions in number of nematodes were significant for all genera ( $P < 0.05$ ). For the most commonly observed genera *Panagrolaimus* and *Rotylenchus*, numbers were by 88% and 95% lower, respectively.

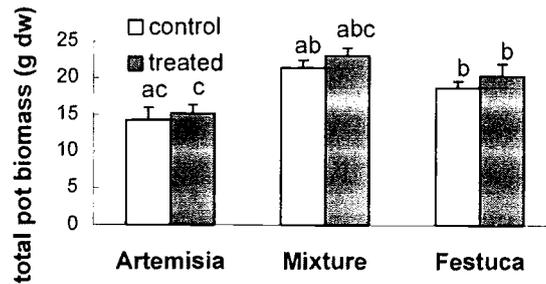
## NUMBER OF NEMATODES IN UNTREATED POTS

The total number of nematodes in untreated pots was high, with around 7000 individuals per 100g of fresh soil (Figure 1). Most nematodes belonged to the genus *Panagrolaimus* (71%), which are opportunistic bacteria-feeders, common to terrestrial grassland systems. Second-most common were plant-parasitic nematodes of the genus *Rotylenchus*, with on average  $\pm 1\ 000$  individuals per 100g (15%). Other genera were less abundant (14%), all together with about 1 000 ind. per 100g. Of those, *Monhystera*, a bacteriophagous nematode with several species in marine environments, was most abundant, followed by *Rhabditis*, *Tylenchus* and *Plectus*.

Density of nematodes in untreated pots did not differ among plant species compositions ( $F_{2, 6} = 0.01$ ,  $P = 0.992$ ). On average, the density of *Rotylenchus* in both *Festuca* and mixture pots was about 5 $\times$  as high as in *Artemisia* pots, but differences were on the edge of significance ( $F_{2, 6} = 4.97$ ,  $P = 0.053$ ). The density of *Rotylenchus* increased with an increase in below-ground plant biomass ( $y = 52.86 \cdot e^{0.19x}$ ,  $R^2 = 0.53$ ,  $F_{1, 7} = 7.91$ ,  $P <$



**Figure 1.** Average number of nematodes per 100g wet soil of nematicide treated and control pots, indicated for the three different plant species compositions separately. Different letters indicate significant differences of total numbers according to LSD test ( $N = 3$ ). Of the 6 genera found, only nematode species of the genus *Rotylenchus* are obligatory plant-parasitic. Nematodes of the genera *Monhystera*, *Panagrolaimus*, *Plectus*, and *Rhabditis* are bacteriophagous, while members of *Tylenchus* are fungivore to root-feeding nematodes. Art = *Artemisia*, Fest = *Festuca*, Mix is mixture of both.



**Figure 2.** Average total plant biomass in pots of the different treatments (g dry weight  $\pm$  SE; above- plus below-ground). Different letters indicate significant differences according to Tukey's hsd of  $\log_{10}$ -transformed data ( $P < 0.05$ ).

0.05), which might explain part of the differences in numbers of *Rotylenchus* between *Artemisia* and *Festuca* or mixture soils. The number of nematodes of other genera did not differ significantly among plant species compositions (all with  $p > 0.20$ ).

### PLANT BIOMASS

Effects of nematicide application on total plant biomass was negligible (Figure 2). While differences among *Festuca*, *Artemisia* and mixture were detected ( $F_{2, 65} = 19.55$ ,  $P < 0.001$ ), we did not find any significant effect of the nematicide treatment on total plant biomass (nematicide application:  $F_{1, 65} = 1.43$ ,  $P = 0.235$ ; interaction:  $F_{2, 65} = 0.01$ ,  $P = 0.989$ ). Moreover, when above- or below-ground biomass were tested separately, no significant effects were found (Table 1). Root-biomass production within the experimental period ranged between 70% (*Artemisia*) and 400% (*Festuca*), supplying the plant-feeding nematodes with high amounts of young roots.

The effects of nematodes on the competitive outcome between *Artemisia* and *Festuca*

**Table 1.** Average dry weight ( $\pm$  SE) of above- and below-ground biomass in the two nematicide treatments separated for the three different plant species compositions. F and P values derive from one-way ANOVA of  $\log_{10}$ -transformed data. Plants in few pots died and were excluded from the analyses (*Artemisia* 2, *Festuca* 1, Mixture 1).

species	plant part	N	control	treated	F	P
<i>Artemisia</i>	above-ground	18	4.15 (0.39)	4.03 (1.46)	0.17	0.685
	below-ground	18	10.19 (1.45)	11.19 (1.46)	0.44	0.515
<i>Festuca</i>	above-ground	19	5.49 (0.33)	5.19 (0.43)	0.42	0.526
	below-ground	19	13.24 (0.67)	15.16 (1.34)	1.14	0.301
Mixture	above-ground	31	6.39 (0.30)	6.47 (0.29)	0.02	0.882
	below-ground	31	15.13 (0.88)	16.86 (0.89)	1.86	0.183

was assessed in pots comprising a mixture of both plant species. The percentage *Artemisia*

**Table 2.** The impact of nematicide application on competition ( $\pm$  SE). Numbers give the final percentage of *Artemisia* in the mixture. F and P values derive from one-way ANOVA of arcsin(square-root)-transformed data. N = 16.

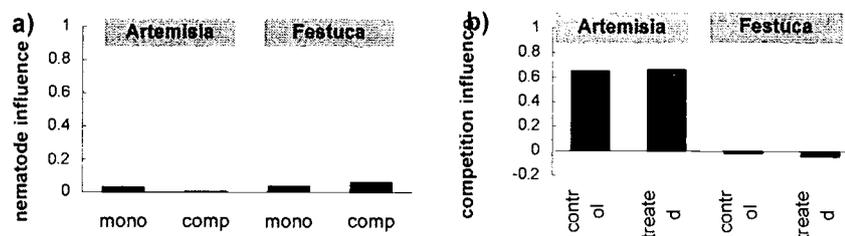
	control	treated	F	P
above-ground	10.37 (1.12)	10.16 (1.64)	0.15	0.702
below-ground	9.83 (0.86)	8.72 (1.21)	0.88	0.354
total	10.13 (0.76)	9.85 (1.32)	0.17	0.684

of total biomass did not change with the application of nematicide (Table 2). Apparently, nematicide addition did not influence the competitive outcome between the two plant species.

Based on the indices of competition and nematode influence, interspecific competition had a much greater impact on the performance of *Artemisia* than had nematodes (Figure 3). While for both plant species the RNI-values were close to zero (indicating no effect of nematicide application), *Artemisia* suffered from the presence of *Festuca* in the mixtures. The RCI was higher than 0.6, meaning a 60%-reduction in *Artemisia* biomass in mixtures relative to monocultures. In *Festuca*, on the other hand, no negative effects of interspecific competition were measured. We therefore conclude that in *Artemisia* the impact of nematodes was overruled by competition, while in *Festuca* none of the two factors influenced its performance.

## DISCUSSION

In this study, we found no effect of nematodes on plant performance. Furthermore, no effect of nematodes on the outcome of plant competition could be established. Despite a large reduction of plant-feeding nematodes (i.e. *Rotylenchus*), we were unable to detect changes in plant performance or competitive outcome. We therefore conclude that below-ground grazing by phytophagous nematodes seems not to play a major role in salt-marsh



**Figure 3.** a) Relative nematode influence (RNI) and b) relative competition influence (RCI) for the two plant species separately. Values for nematode influence are all close to zero, meaning no differences in plant biomass between treated and control pots. Values for competition influence in *Artemisia* deviate from zero, indicating a reduction in growth for plants in competition relative to single-species stands. In *Festuca*, no such effect was observed.

parts dominated by *Festuca rubra* or *Artemisia maritima* as found on the island of Schiermonnikoog.

A large number of studies emphasised the effects of nematodes on plant performance (as reviewed by Stanton 1988). Although many studies derive from an agricultural context, similar patterns are found in natural systems (Stanton et al. 1981, Ingham et al. 1985, 1986b, Van der Putten et al. 1993, De Rooij-Van der Goes 1995, Van der Putten & Peters 1997). Despite the impact of below-ground nematodes on plant performance, no effects on the outcome of plant competition were found in any of the field experiments we are aware of (Chen et al. 1995, Ponce et al. 1995, Van der Veen et al. in prep). In just a single study, leaf-feeding nematodes were shown to shift the competitive balance between plant species (Pantone et al. 1989, but see Pantone 1995).

The lack of a measurable effect in the present study of nematodes on plant performance can not be attributed to low nematode densities. The total number of nematodes as well as the number of plant-parasitic nematodes were high, relative to other systems (cf. Sohlenius & Sander 1987). In the untreated salt-marsh soil, around  $9 \cdot 10^6$  ind.  $\cdot$  m<sup>-2</sup> were found, which is equivalent to a nematode biomass of nearly 1 000 mg per m<sup>2</sup> (conversion factor: 0.11  $\mu$ g ind<sup>-1</sup> - Sohlenius & Sander 1987). On average, total nematode biomass in terrestrial ecosystems ranges between 120 and 450 mg  $\cdot$  m<sup>-2</sup> (Peterson 1982b), which is less than half of our counts. Grasslands harbour on average more nematodes than any other terrestrial system, with 0.9 to  $9 \cdot 10^6$  ind.  $\cdot$  m<sup>-2</sup> as typical density in temperate regions (Peterson 1982a). This means that the density in our salt marsh ( $\pm 9 \cdot 10^6$  ind.  $\cdot$  m<sup>-2</sup>) is high even for grasslands. Data from the lower end of a salt marsh in Georgia, USA, indicate a lower density, in the range of 1 to  $6 \cdot 10^6$  ind.  $\cdot$  m<sup>-2</sup> (Teal & Wieser 1966).

Several factors might have prevented the detection of nematodes affecting plant performance and plant competition. Although we used intact sods in the experiment, conditions might have differed from the situation in the field. Since we prevented soils from drying out, conditions might have been too benign to let the plants suffer from nematode grazing (cf. Mortimer et al. 1998). To measure impact of plant-feeding nematodes by means of chemical perturbation experiments is very much a black-box approach. Application of nematicide not only caused a reduction in the number of plant-parasitic nematodes, but also other groups of nematodes were diminished. A decline in the number of leaf-degrading nematodes may result in less nitrogen available to plants due to a decreased decomposition rate (Alkemade et al. 1993), with suppressed plant growth as a consequence. Also by diminishing the number of bacteria-feeding nematodes, the whole nutrient turn-over might be suppressed (Yeates & Coleman 1982, Stanton 1988), thereby outbalancing the positive effect of ceased grazing by plant-parasitic nematodes. The perturbation studies conducted by Ingham et al. (1985, 1986a,b) and Stanton et al. (1981), in which certain groups of below-ground organisms were removed from the soil community, indicated the opposite: Plant shoot biomass as well as shoot nitrogen content increased.

These type of perturbation experiments therefore, can only be the start of more detailed studies, dealing with groups of species, i.e. inoculated into sterile ground (see Van der Putten and Van der Stoel 1998). Furthermore, these experiments should also be performed

in the field, and not only with potted soils from the field, and the time span should be adapted to the speed of the processes under study, which is in case of plant competition one or more years, instead of several months.

Despite the shortcomings of the study, we regard it to be unlikely that our findings can be explained by a series of counteracting knock-on effects, without any consequences for plants and their interactions. The lack of response of the plants to the release from nematode grazing, hence, suggests nematodes to be only of minor importance to salt-marsh vegetation dominated by *Artemisia maritima* and *Festuca rubra*.

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## REFERENCES

- Alkemade, R., Wielemaker, A. and Hemminga, M. A. 1993. Correlation between nematode abundance and decomposition rate of *Spartina anglica* leaves. - Mar. Ecol. Prog. Ser. 99: 293-300.
- Andrzejewska, L. and Gyllenberg, G. 1980. Small herbivore subsystems. - In: Breymeyer, A. J. and van Dyne, G. M. (eds.), Grasslands. Systems analysis and man. Cambridge Univ. Press, Cambridge, pp. 201-267.
- Bakker, J. P., Esselink, P., van der Wal, R., and Dijkema, K. 1997. Options for restoration and management of coastal salt marshes in Europe. - In: Urbanska, K. M., Webb, N. R. and Edwards, P. J. (eds.), Restoration ecology and sustainable development. Cambridge Univ. Press, Cambridge, pp. 286-324.
- Bonser, S. P., and Reader, R. J. 1995. Plant competition and herbivory in relation to vegetation biomass. - Ecology 76: 2176-2183.
- Brown, V. K. 1990. Insect herbivory and its effect on plant succession. - In: Burden, G. G. and Leather, S. R. (eds.), Pest, pathogens, and plant communities. Blackwell, Oxford, pp. 275-288.
- Chen, J., Bird, G. W. and Renner, K. A. 1995. Influence of *Heterodera glycines* on interspecific and intraspecific competition associated with *Glycine max* and *Chenopodium album*. - J. Nematol. 27: 63-69.
- De Rooij-Van Der Goes, P. C. E. M. 1995. The role of plant-parasitic nematodes and soil-borne fungi in the decline of *Ammophila arenaria* (L.) Link. - N. Phytol. 129: 661-669.
- Drent, R. and van der Wal, R. 1998. Cyclic grazing in vertebrates and the manipulation of the food resources. - In: Olf, H., Brown, V. K. and Drent, R. H. (eds.), Plants, herbivores and predators. Blackwell, Cambridge, in press.
- Gates, D. J., Westcott, M., Burdon, J. J., and Alexander, H. M. 1986. Competition and stability in plant mixtures in the presence of disease. - Oecologia 68: 559-566.

- Griffin, G. D. 1984. Nematode parasites of alfalfa, cereals, and grasses. - In: Nickle, W. R. (ed.), Plant and insect nematodes. Marcel Dekker, New York, pp. 243-321.
- Ingham, E. R., Trofymow, J. A., Ames, R. N., Hunt, H. W., Morley, C. R., Moore, J. C. and Coleman, D. C. 1986a. Trophic interactions and nitrogen cycling in a semi-arid grassland soil. I. Seasonal dynamics of the natural populations, their interaction and effects on nitrogen cycling. - J. Appl. Ecol. 23: 597-614.
- Ingham, E. R., Trofymow, J. A., Ames, R. N., Hunt, H. W., Morley, C. R., Moore, J. C. and Coleman, D. C. 1986b. Trophic interactions and nitrogen cycling in a semi-arid grassland soil. II. System responses to removal of different groups of soil microbes or fauna. - J. Appl. Ecol. 23: 615-630.
- Ingham, R. E., Trofymow, J. A., Ingham, E. R. and Coleman, D. C. 1985. Interaction of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. - Ecol. Mono. 55: 119-140.
- Mortimer, S. R., Van der Putten, W. H., and Brown, V. K. 1998. Insect and nematode herbivory below-ground: interactions and role in vegetation succession. - In: Olf, H., Brown, V. K. and Drent, R. H. (eds.), Plants, herbivores and predators. Blackwell, Cambridge, in press.
- Olf, H., de Leeuw, J., Bakker, J. P., Platerink, R. J., van Wijnen, H. J. and de Munck, W. 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. - J. Ecol. 85: 799-814.
- Pantone, D. J., Williams, W. A. and Maggenti, A. R. 1989. An alternative approach for evaluating the efficacy of potential biocontrol agents of weeds. 1. Inverse linear model. - Weed Sci. 37: 771-777.
- Pantone, D. J. 1995. Replacement series analysis of the competitive interaction between a weed and a crop as influenced by a plant parasitic nematode. - Fundam. appl. Nematol. 18: 81-85.
- Peterson, H. 1982a. Structure and size of soil animal populations. - Oikos 39: 306-329.
- Peterson, H. 1982b. The total soil fauna biomass and its composition. - Oikos 39: 330-339.
- Ponce, R. G., Zandaca, C., Verdugo, M. and Salas, L. 1995. The influence of the nematode *Meloidogyne incognita* on competition between *Solanum nigrum* and tomato. - Weed Res. 35: 437-443.
- Powers, L. E., McSorley, R., Dunn, R. A. and Montes, A. 1994. The agroecology of a cucurbit-based intercropping system in the Yeguaré Valley of Honduras. - Agricult. Ecosys. Environ. 48: 139-147.
- Price, P. W., Westoby, M., Rice, B., Atsatt, P. R., Thompson, J. N. and Mobley, K. 1986. Parasite mediation in ecological interactions. - Ann. Rev. Ecol. Syst. 17: 487-505.
- Smolik, J. D. 1977. Effect of nematicide treatment on growth on range grasses in field and glasshouse studies. - In: Marshall, J.D. (ed.), The below-ground ecosystem: a synthesis of plant-associated processes. Range Sci. Dep. Sci. Ser. 26. Colo. State Univ., Ft. Collins, pp. 257-260.
- Sohlenius, B. and Sander, A. 1987. Vertical distribution of nematodes in arable soil under grass (*Festuca pratensis*) and barley (*Hordeum disticum*). - Biol. Fertil. Soils 3: 19-25.
- Stanton, N. L. 1988. The underground in grasslands. - Ann. Rev. Ecol. Syst. 19: 573-589.
- Stanton, N. L., Allen, M. and Champion, M. 1981. The effect of the pesticide carbofuran on soil organisms and root and shoot production in shortgrass prairie. - J. Appl. Ecol. 18: 417-431.
- Southey, J. F. 1986. Laboratory methods for work with plant and soil nematodes. - 6th edition. Reference Book 402. HMSO, London.
- Teal, J. M. and Wieser, W. 1966. The distribution and ecology of nematodes in a Georgia salt marsh. - Limno. Oceanogr. 11: 217-222.
- Van Der Putten, W. H., and Peters, B. A. M. 1997. How soil-borne pathogens may affect plant competition. - Ecology 78: 1785-1795.
- Van der Putten, W. H. and Van der Stoep, C. D. 1998. Plant parasitic nematodes and spatio-temporal variation in natural vegetation. - Applied Soil Ecology, in press.

- 
- Van Der Putten, W. H., Van Dijk, C. and Peters, B. A. M. 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. - *Nature* 362 : 53-56.
- Van der Veen, A., Kaldeway, C. and Bakker, J. P. submitted. Above- and below-ground herbivory affect plant competition along a successional gradient of dry coast sand dunes.
- Van der Wal, R., Egas, M., Van der Veen, A. and Bakker, J. P. submitted. Effects of resource competition and herbivory on plant performance along a productivity gradient.
- Van Wijnen, H. J., van der Wal, R. and Bakker, J. P. submitted. The impact of small herbivores on nitrogen mineralization rate: consequences for salt-marsh succession.
- Weaver, T. and Smolik, J. 1987. Soil nematodes of northern Rocky Mountain ecosystems: genera and biomasses. - *Great Basin Naturalist* 47: 473-479.
- Westhoff, V. and Den Held, A. J. 1969. *Plantengemeenschappen van Nederland*. - Thieme, Zutphen.
- Yeates, G. W. and Coleman, D. C. 1982. Nematodes and decomposition. - In: Freckman, D. W. (ed.), *Nematodes in soil ecosystems*. Univ. of Texas Press, Austin, pp. 55-80.



## EPILOGUE

In Europe, we can find Nature, in the sense of not directly manipulated parts of our environment, only in remote places. The expansion of our population as well as the action of an ever-growing economy restricts the occurrence of organisms in their natural environment to the alpine meadows of the Alps, some boreal forests in Scandinavia, major parts of the arctic, and, to a lesser extent, to salt marshes along the Wadden Sea coast. Only here the direct activities of mankind are of minor impact. However, all ecosystems of the world are interconnected, and the atmospheric deposition of nitrogen, sulphur, dust and radioactive particles, the consequences of mobility, i.e. higher CO<sub>2</sub>-content of the atmosphere, and the traces of a comfortable and wealthy life as PCBs and CFCs are detectable and influential all around the world.

This is the attitude with which I came to work on the small Dutch island Schiermonnikoog, an island in the over-fished and oil and gas drilled North Sea. I doubted that my study would actually deal with natural processes. But despite the military jets that occasionally flew over the island, despite the flames of a gas pump station on the mainland in sight, and even despite the plastic debris washed upon the shore, I now think of the salt marsh of Schiermonnikoog as a natural system.

The results of the studies presented here were to my opinion worth the effort, because they are drawn from an environment not overruled by agriculture and forestry, thus might represent natural processes. To me, it seems important to realise that ecological studies in man-made landscapes are pressed into a functional interaction that would not occur naturally. The coexistence of species-diverse grasslands are products of tens of years of extensive mowing or grazing management. If naturally occurring herbivory would have the same effect is questionable.

Still, investigating a natural system is an ecological luxury. The pleasure and satisfaction I took from working here is paid by the restriction of access during the bird breeding season, which is a constant point of disharmony between the islanders and the intruding scientists. Just like fine art, the art of science will only be accepted and paid by the public if they see a gain in it. It would be usurping to hope that the findings in this report counterbalance the disturbance I caused in the vegetation and in the inhabitants of the island.

The inhabitants of Schiermonnikoog and the workers of Natuurmonumenten are gratefully acknowledged for given me the opportunity to work on their island.

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