Summary

Different theories have been postulated about how plant-herbivore interactions will change along gradients of plant productivity. They lead to different predictions on the importance of top-down and bottom-up effects in structuring communities. The classical exploitation theory predicts increasing top-down control along a gradient of primary productivity. At intermediate levels of productivity, herbivores will regulate plant biomass, whereas at high levels of productivity herbivores will be regulated by carnivores. In contrast, the quality threshold theory predicts that bottom-up effects become of more importance at high productivity. Decreasing plant quality will result in decreasing herbivore numbers. Both theories predict that herbivores will have the strongest impact on the vegetation at intermediate levels of productivity.

The main aim of this thesis is to study how plant-herbivore interactions change along a natural productivity gradient at the island of Schiermonnikoog. Due to the eastward expansion of this island a range from young unproductive salt marshes to old productive marshes can be found in a choronosequence representing succession. Two types of small herbivores occur on the salt marsh: migrating geese (barnacle geese: *Branta leucopsis* and brent geese: *Branta bernicla*) and resident brown hares (*Lepus europaeus*). All these herbivores show an optimum at marshes of intermediate productivity. Predation by carnivores on hares and geese is very rare in the salt marsh.

Two plant species which dominate different stages of salt-marsh succession, *Festuca rubra* from young marshes and *Elymus athericus* from old marshes, were selected for a greenhouse experiment (**Chapter 2**). We tested how the competitive balance between both species was affected by simulated grazing under different levels of soil nitrogen. The competitive balance was shifted towards the species which allocated most of its biomass to stem tissue (*Elymus athericus*) at high levels of nitrogen. Clipping did not change the outcome of competition even though more biomass was removed than observed under field conditions. This suggested that herbivory could retard the spread of this species mainly by affecting the establishment, and not by grazing after it had established.

The effects of herbivory and interspecific plant competition on the establishment of *Elymus athericus* were studied in a field experiment (**Chapter 3**). Seedlings were transplanted at sites with a different successional age. Competition reduced growth of seedlings and the effect of competition increased with salt-marsh age. Herbivory (mainly by hares **Box 3.1**) strongly reduced survival. The largest reduction in survival was found at the youngest salt marsh. Grazing thus mainly affects the establishment of this late successional species.

In **Chapter 4** the long-term impact of herbivory on salt-marsh vegetation succession was studied. Excluding both geese and hares resulted in the largest changes in species composition in young salt marshes. At these sites, typical late successional species, such as *Atriplex portulacoides* and *Elymus athericus* became established after seven years in the absence of herbivores. Only excluding geese did not affect the species composition of the vegetation. The same patterns of vegetation development were observed on two islands where no hares have been present (but geese did occur) since the beginning of salt-marsh formation (**Chapter 5**). Thirty years of succession had led on both islands to a dominance of *Atriplex portulacoides* on the low marsh and *Elymus athericus* on the high salt marsh. Stages dominated by both species can only be found on marshes of more than 50 years old on the grazed salt-marsh system at Schiermonnikoog. This leads to the conclusion that grazing by mainly hares can retard vegetation succession for at least 20 years. However, hares cannot prevent the invasion of these late successional species with increasing levels of soil nitrogen. Old productive marshes show a high dominance of both plant species. The presence of tall less palatable plants has a negative effect on the grazing intensity by hares (**Box 6.1**), hence old marshes have a low numbers of hares.

Cattle grazing on these old marshes leads to a reduction of these tall-growing plants and to a return of a short vegetation with a high abundance of preferred food plant species. Cattle thus facilitate suitable foraging sites for both geese and hares (**Chapter 6**). Small herbivores, such as hares and rabbits, have several adaptations in their digestive system that cope with low quality forage (**Chapter 7**). However, when tall plants will dominate the marshes, with increasing productivity, the small herbivores will disappear. Although they control the vegetation at the unproductive sites, they have lost control at the highly productive sites. At these sites they need the help of a large herbivore to top-down regulate the vegetation.

In contrast to previous theories we find that top-down effects decrease and bottom-up effects increase along a gradient of plant productivity (**Chapter 8**). Hence, small herbivores, such as geese and especially hares, have the strongest impact on the vegetation in low-productive stages of the productivity gradient. This can be explained by the selective grazing of the herbivores, which prevent establishment at the unproductive stages of succession.