Nitrogen dynamics and vegetation succession in salt marshes

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SUMMARY

In this thesis, I compose a nitrogen budget for coastal-barrier salt marshes in the Wadden Sea, and describe the effects of increased nitrogen levels on plant-species composition and plant biomass. Also, herbivore effects on plant characteristics and nitrogen cycling are considered. An important input of nitrogen in these salt marshes is via sediment deposition. There is a large amount of spatial variation in deposition rate, with a higher rate towards low-marsh sites where inundation frequency is higher. Also, temporal variation is high, with highest deposition rates in young marshes. During the first 100 years of marsh development marsh surface elevation increases faster than sea level rise, which results in a reduced inundation frequency. After 100 years, sea level rise is faster than marsh surface increment due to shrinkage of the clay layer, which threatens low-marsh sites in the long term. Cliff formation in the pioneer zone might be the result. Active plant uptake of inorganic nitrogen during seawater inundation is probably an important second input of nitrogen, but which was not measured in this thesis. Dissolved organic nitrogen is probably exported, but again was not measured. Export of dissolved organic nitrogen may compensate for the imported sediment organic nitrogen. In addition to tidal deposition, atmospheric deposition is an important inorganic nitrogen input in salt marshes and which increases during succession as a result of higher plant canopy. Wet deposition of nitrate and ammonium was 1.7 g N m^{-2} yr^{-1}, whereas throughfall deposition (dry and wet deposition) ranged between 2.1 g N m^{-2} yr^{-1} and 3.6 g N m^{-2} yr^{-1}, and which was positively related to the height of plant canopy. In total, nitrogen is imported in coastal barrier marshes in the Wadden Sea, with the highest input at a low elevation in young marshes.

In order to quantify the importance of nitrogen for plant characteristics in these marshes, a factorial fertilizer experiment was conducted in a 15-year-old marsh with a low soil nitrogen content and in an older 100-year-old marsh with higher nitrogen content. It was expected that older marshes are released from N limitation, since they become enriched with nitrogen. Plots were fertilized at high and low marsh elevations in both marshes. Nitrogen and phosphorus were applied at low and high concentrations both separately and in combination in each of three successive years. Nitrogen limited above-ground plant growth in both young and old salt marshes in all years. Phosphorus limitation of plant growth was apparent in the first year in the young marsh and in the last year in both marshes. In young marshes with low soil organic matter, phosphorus limitation may occur. In addition, phosphorus limitation occurs at both

successional stages when a marsh is saturated with nitrogen. Plant species that are typical of nitrogen-rich habitats and late successional stages significantly increased in biomass after fertilization. *Limonium vulgare*, a low stature species of early and intermediate successional stages, decreased in biomass whereas the taller *Elymus pycnanthus* and *Artemisia maritima* increased. After 3 years of fertilization, plant species composition in a young marsh was similar to the species composition in an unfertilized older marsh, which implies that fertilization increased the rate of vegetation succession. Fertilization of a 100-year-old marsh in *Festuca rubra* - *Juncus gerardi* vegetation, however, still resulted in a change in plant species composition, suggesting that succession was still occurring and that, overall, plants in marshes of different age are similar in their response to fertilization. Results from fertilization studies, however, are highly dependent on initial plant species composition, and previous fertilization experiments in these coastal barrier marshes did not lead to any plant response, probably because fertilization was carried out in *Halimione portulacoides* vegetation. Since *Halimione portulacoides* becomes more dominant at later successional stages, it is likely that, overall, older marshes are released from N limitation.

Nitrogen mineralization rate is an important flux, which determines to a large extent the amount of plant-available nitrogen. Since these coastal barrier marshes were found to be limited by nitrogen, increased mineralization rates may result in higher plant uptake. N-mineralization rate increased during succession. In general, nitrogen accumulates in the plant and soil compartment over time, which enables a higher mineralization rate. Net nitrogen mineralization rate was low in young marshes and increased towards 8 - 13 g N m^{-2} yr^{-1} at sites with high nitrogen content in the plant and soil compartment. These sites can particularly be found in old marshes at a low elevation. Temporal variation in mineralization rate seems to be higher than spatial variation, although only intermediate and low-marsh sites were taken into account. Mineralization rates in general are higher at high-marsh sites when results from literature are taken into account. This may indicate that salinity and anoxic conditions reduce mineralization rates. Differences between mainland marshes and coastal-barrier marshes in the Wadden Sea are small. Mineralization rates were slightly higher on Schiermonnikoog, but this effect is probably due to the longer extraction period used.

Herbivore effects (geese and hares) on mineralization rates are considerable. Mineralization rate was significantly higher at ungrazed than at grazed sites. In the absence of grazing, mineralization rate increased over the course of succession, whereas it remained relatively low when sites were grazed. The amount of plant litter was significantly lower at grazed sites. In addition, the amount of litter and potential litter (non-woody, live shoots) was linearly related to net N-mineralization rate. This implies that herbivores reduced mineralization rate by preventing litter accumulation. Bulk density was higher at grazed salt-marsh sites than at ungrazed sites. This factor may also have contributed to the differences in net N-mineralization rate between grazed and ungrazed sites. Where small herbivores such as geese and hares are not able to reset the successional clock, larger herbivores can. They were found to decrease dominance of *Elymus pycnanthus* and provided favourable conditions for early successional species to become dominant. In addition to direct effects of these larger herbivores on plant-species composition, they considerably reduced mineralization rate also.

A dynamic annual nitrogen budget was made for a young and old salt marsh at a high and low elevation. Plant-species dominance changed along the successional sequence. In early stages, *Elymus farctus* and *Spergularia media* occupied a large part of total plant biomass. *Festuca rubra* and *Puccinellia maritima* were dominant at intermediate stages, whereas *Elymus pycnanthus* and *Limonium vulgare* were dominant at late stages of succession. Shoot biomass was highest in June, whereas litter biomass was highest in September and December. Root biomass formed by far the largest fraction of total plant biomass, especially at a low-marsh elevation. In general, shoot N-concentration was highest in December and March and decreased during the growing season. At a low-marsh elevation, plant N-availability depended equal amounts on tidal N, atmospheric N and mineralized N in young marshes, whereas the decomposition pathway became more important in older marshes. Tidal N contributed most to ecoystem N-accumulation rate at early successional stages, whereas atmospheric N was more important at later stages. Tidal influence was low at high-marsh elevation sites. Here, atmospheric deposition was the dominant exogenous nitrogen source both in young and old marshes.