Summary

The subject of this thesis is the identification of feedback mechanisms that can slow down nutrient accumulation in pioneer stages of dune slack succession and/or prevent the establishment of fast-growing, later successional species. This elongates the life span of early successional stages that harbor many endangered plant species.

Succession in wet dune slacks has been a research topic in Northwest Europe for more than half of a century. At first, the work focussed on the successional relations of the different vegetation types. But with increasing knowledge the central question that emerged was which key factors are the driving force of the observed succession. Nutrient accumulation, the hydrological regime, herbivory, and acidification were distinguished as key factors in the ecosystem development of wet dune slacks.

Succession can evolve gradually from bare soil via pioneer and intermediate stages to a climax stage. However, in some cases the vegetation development is inhibited in early stages of succession in dune slack ecosystems. With a combined theoretical and experimental approach we aimed at identifying mechanisms that can modify the key factors in dune slack ecosystem development in such a way that they can explain the observed discontinuous behavior. The approach consisted of three steps;

- Identifying possible mechanisms in the field
- Conducting experiments to test hypothesized mechanisms
- Exploration of the effects of the proposed mechanism by minimal mathematical models

A field survey in the ‘Buiten Muy’, a wet calcareous dune slack on the Frisian Island of Texel gave evidence for the occurrence of positive-feedback switches in dune slack ecosystem development (Chapter 2). It appears that in this dune slack alternative stable states occur. An early pioneer stage (0.5 kg m$^{-2}$ total standing crop) and a more-productive later successional stage (2.9 kg m$^{-2}$ total standing crop) occur side-by-side, with sharp boundaries between them. The
pioneer vegetation has been recorded at the site for more than 62 years. This particular dune slack, where both successional stages occurred, showed no differences in initial abiotic and hydrological conditions. Therefore, biotic interactions were suggested to explain the differences in vegetation development.

We hypothesized that the occurrence of microbial mats and radial oxygen loss (ROL) by early successional species are possible features of the dune slack ecosystem that could induce positive-feedback switches. In Chapters 3 and 4 we focused on the effects of the occurrence of a microbial mat on vegetation development in dune slack ecosystems. In Chapter 3 we looked at the germination and seedling survival of typical dune slack species in the presence of a microbial mat. These dune slack species were separated in early- and late successional species to test the hypothesis that microbial mats inhibited the establishment of late successional species. Though there were large differences in germination rates between species, most species germinated better without a microbial mat. Only the germination of Agrostis stolonifera appeared to be stimulated by the presence of a well-developed microbial mat. Seedlings placed on top of a microbial mat showed a lower survival rate for most species compared to seedlings placed on top of sand or seedlings planted in the mat or in sand. Since the seedlings placed on top of the mat were prevented from drying out, microbial mats apparently formed a physical barrier for roots of seedlings. Despite different species responses, we could not detect general differences in the germination and seedling survival between early and late successional species. An indication for differences between the successional groups was only found in plant growth. Species of the early and intermediate successional stages grew significantly better if a microbial mat was present, whereas a late successional species was not stimulated. An explanation for this may be that the earlier species can profit from the slightly enhanced nitrogen availability caused by N2-fixation of cyanobacteria in the microbial mat. The enrichment of the soil with nitrogenous and also organic compounds stimulates the activity of micro-organisms in the soil. This may result in anoxic soil conditions followed by the production of the toxic sulfide by sulfate-reducing bacteria.

Consequences of sulfide toxicity on the succession in wet calcareous dune slacks were investigated in Chapter 4. Sulfide may exert an inhibitory effect on dune slack species, but several pioneer plants exhibit ROL and can, therefore, protect themselves against free sulfide. Late successional species not capable of ROL may be sensitive to free sulfide and cannot invade the area. If so, such phenomena have a stabilizing effect on the pioneer vegetation. A mesocosm experiment was set up to test if sulfide becomes toxic in wet dune slack succession. Also, in situ data were collected in a dune slack on the Frisian Island of Texel. Free sulfide was studied in mesocosm experiments in Carex nigra with and without ROL. That sulfide in mesocosms without ROL may be taken into account.

In the field, the groundwater at the salt marsh site showed large amounts of free sulfide. Differences in biotic interactions because of free sulfide may induce this difference between the two stages.

The sulfide concentrations were too low to have toxic effects on the vegetation. This suggests that free sulfide is not a limiting factor in the succession because secondary species can protect themselves against sulfide toxic effects. The sulfide concentration at the salt marsh site was too low to have toxic effects on the vegetation. This suggests that free sulfide is not a limiting factor in the succession because secondary species can protect themselves against sulfide toxic effects. The sulfide concentration at the salt marsh site was too low to have toxic effects on the vegetation. This suggests that free sulfide is not a limiting factor in the succession because secondary species can protect themselves against sulfide toxic effects.
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Chapters 3 and 4

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The sulfide concentrations measured at the infiltration site of the slack were too low to harm Phragmites australis, a late successional dominant species that covered this area. This species can even be favored by the low sulfide concentrations because it can increase the phosphate availability by competition for binding places to iron and calcium. Therefore, the results from the field suggested that free sulfide accelerates the succession, rather than slow it down.

ROL from the roots does not only protect against toxic conditions in anaerobic soils. Oxygen release could have an influence on abiotic soil parameters and therefore affect the competitiveness of species. In Chapter 5 we studied the effects of typical dune slack plants on nutrient concentrations of the soil solution. This mesocosm experiment with Littorella uniflora and Carex nigra, as ROL and non-ROL species respectively, revealed remarkable differences in soil solution parameters. Special attention was given to nitrogen because this nutrient is often mentioned as the limiting resource in dune slack succession. Mesocosms with Littorella uniflora showed a higher nitrate concentration in the soil than mesocosms with Carex nigra and the control. Moreover, a significantly higher fraction of nitrogen was missing in Littorella uniflora (58%) than in Carex nigra (5%) mesocosms estimated at the end of the experimental period. The observed enhanced nitrogen losses in mesocosms with Littorella uniflora could result in a positive-feedback mechanism. Succession theory predicts that during primary succession competition for nutrients shifts to competition for light. Therefore, early successional species can extend their life span if they can retard the nutrient accumulation in the system. Such a process is called a positive-feedback switch.

In Chapter 6 enhanced nitrogen loss, as a potential cause of a positive feedback switch was further explored. Two early successional species capable of Texel. Free sulfide was detected only at nighttime in mesocosms populated by Carex nigra, a late successional species, and in unvegetated units, but not in mesocosms vegetated with Littorella uniflora, a pioneer species capable of ROL. That sulfide is only found during the night indicates that when investigating sulfide toxicity besides spatial differences also temporal differences have to be taken into account.

In the field, sulfide and redox profiles showed distinct differences between the groundwater exfiltration and infiltration sites of the dune slack. At the exfiltration site, sulfide was found only occasionally. In contrast, measurable amounts of free sulfide were regularly found at the infiltration site of the slack. Differences in availability of iron and calcium in the groundwater appeared to cause this difference between sites. These two compounds can bind free sulfide to iron sulfide and calcium sulfide, which are harmless for plants.

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of ROL were compared to two non-ROL species for their denitrification rates in a mesocosm experiment. Denitrification rates in mesocosms of both early successional species *Littorella uniflora* (30 times; \( P<0.001 \)) and *Schoenus nigricans* (10 times; \( P<0.05 \)) were significantly higher than in mesocosms with the non-ROL species, *Carex nigra* and *Calamagrostis epigejos*. Secondly, analysis of the concept of enhanced nitrogen loss by a simple theoretical model revealed that early successional species capable of ROL may initiate a positive-feedback switch at limited nitrogen input levels. Under these circumstances there is no further succession and the ecosystem is locked in an unproductive state for an extended period of time. Enhanced nitrogen loss, acting as positive-feedback mechanism, can explain why the area of low-productive vegetation has rapidly declined the last decades. Lowering of the water table and increased atmospheric deposition of nitrogen had diminished the effects of enhanced nitrogen loss on retarding ecosystem development.

In the Enhanced-nitrogen-loss model we assumed a linear relationship between enhanced nitrogen loss and plant biomass. However, this is only accurate for low biomass levels. At high biomass levels denitrification will decrease because of complete aeration of the soil as found in a preliminary denitrification experiment. This indicates that enhanced nitrogen loss is restricted to limited nitrogen levels, not only because of the increased compatibility of the later successional species but also because the nitrogen loss will decrease at high biomass levels of the early successional species.

The high atmospheric nitrogen loads may have overruled the importance of enhanced nitrogen loss in wet dune slack succession nowadays. Nevertheless, it might had been an important feedback mechanism in the past when the atmospheric nitrogen loads were much lower. The Dutch Government wants to reduce the nitrogen emissions by 50 % in 2010, indicating that effects of enhanced nitrogen loss on ecosystem development may recover in the future.