On the mechanisms of vegetation succession

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Summary

The present study was set up in order to investigate mechanisms of succession, meaning the explanation of species dynamics from the underlying process (e.g. colonization, nutrient dynamics, resource competition, vegetation structure). We investigated species dynamics during succession, quantified the compartmentation of nutrients, and measured N mineralization. Differences between species in growth and allocation characteristics were investigated in greenhouse experiments. Nutrient addition experiments in the field were performed in order to assess which nutrients limit productivity, and to see if different species were limited by different nutrients.

Three research areas were selected which clearly differed in the landscape-level boundary conditions for vegetation succession:

(i) Grasslands which are cut annually, and are located in the Drentse A Nature Reserve, the Netherlands (53°N, 6°42'E), where succession started after the application of fertilizers to these grasslands was stopped,

(ii) Dunes and dune slacks on the island of Schiermonnikoog, the Netherlands (53°29'N, 6°12'E), where vegetation succession started on bare soil in a beach plain area,

(iii) The salt marsh of the island of Schiermonnikoog (53°29'N, 6°42'E) where vegetation succession started on bare sand plates in the Wadden sea, and herbivores played an interesting role since the area was important for spring staging of Brent geese (*Branta bernicla*).

The last two sites are relatively free from human impact, so that undisturbed successional sequences up to 100 years could be reconstructed. The Drentse A area has a long history of agricultural use of the grasslands.

Succession in the grassland series proceeded with decreasing productivity, decreasing pool sizes of N and P in the soil, decreasing N mineralization and quick species replacement. Species diversity was highest in the last successional stage which was characterized by multiple nutrient limitation. Since furthermore different species responded differently to various nutrients, different species might be limited by different nutrients, which might partly explain the high species diversity in this field. We did not find the expected trade-off from species with high allocation to shoots in the productive stages, to species with high allocation to roots in the unproductive stages. Instead, allocation patterns were very plastic within species, which differed mainly in shoot architecture. The most successful species under productive conditions seemed to be the tallest species which can increase their specific leaf area under conditions of light limitation.

Succession in the coastal dunes proceeded with increasing accumulation of nitrogen in the soil and in the ecosystem. A fertilizer application experiment in an early successional stage revealed that the vegetation was mainly limited by

N in this stage. During succession, taller species replaced smaller species, while light interception increased. This suggests an increasing importance of light competition with increasing accumulation of N in the ecosystem.

The distribution of plant species on the salt marsh was found to be determined by two important processes: elevation towards sea-level and successional age. Contrary to the prevailing opinion, these factors appeared to be relatively independent. Succession on the low salt marsh proceeded with a high rate of N accumulation in the soil, which was higher than in the dune system. This higher value is probably caused by a higher input rate by the sediment. Brent geese showed a clear preference for species occurring in a specific early successional stage, low on the salt marsh. This preference is discussed with respect to the expected effects of salinity and nitrogen accumulation on phytomass production and quality.