Basophilous pioneer vegetation in dune slacks on the Dutch Wadden Sea islands
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SUMMARY

The central issue of this thesis is the identification of key factors controlling the occurrence of basiphilous pioneer vegetation in dune slacks on the Dutch Wadden Sea islands. Such vegetation harbours many rare and protected plant species, among which are several orchids, rushes and sedges. In most of North West Europe the characteristic plant communities of natural and semi-natural landscapes are only present in a degenerate form, i.e. the characteristic species are absent or seriously threatened. On the Wadden Sea islands, however, the perspectives for conservation and restoration of several plant communities are comparatively good. This study focuses on a thorough understanding of the necessary habitat conditions for basiphilous species; in particular, the factors which control such conditions: i.e. the key factors.

Initially, in chapter 2, the identification of key variables indicating the presence of a buffer mechanism capable of maintaining the soil-pH above 6.0 (which is generally considered a minimum value for most basiphilous species) is discussed. Chloride and calcium contents of shallow groundwater and the CaCO₃ content of the mineral soil appeared to be key variables. When at least one of these three variables exceeded a certain threshold value, the necessary buffer status appeared to be guaranteed. Moreover, the values of the three key variables together gave information on the type of active buffer mechanism responsible for the environmental control of basiphilous pioneer vegetation: (i) high Cl⁻ and Ca²⁺ concentrations indicate periodical inflow of brackish water, (ii) high CaCO₃ values and Ca²⁺ concentrations indicate the presence of lime-rich mineral soil at the surface, (iii) high Ca²⁺ concentrations combined with low CaCO₃ values and low Cl⁻ concentrations mark the influence of seepage of mineral-rich water originating from larger hydrological systems. The longevity of basiphilous pioneer vegetation appeared to depend on the type of buffer mechanism. For primary dune slacks, on lime-rich soils and/or periodically influenced by brackish water, life span estimates ranged from 30-50 years without a mowing regime to 100-150 years with a mowing regime. If hydrological systems supplied calcareous and iron rich groundwater to slacks, their magnitude and strength determined the life span of basiphilous pioneer vegetation: estimates varied between 20 and 200 years.

The analysis of a hydrological data set from dune slacks on the Dutch Wadden Sea islands Ameland, Terschelling, Vlieland and Texel revealed three variables describing site-specific hydrological conditions (chapter 3), i.e. variables adequately identifying differences in local hydrological conditions between sites. They were inferred by filtering the influences of climatological fluctuations. The site-specificity of the variables could be confirmed by a good fit of modelled (based on these variables in
tors controlling the Dutch Wadden Sea species, among which the characteristic species, only present in a threatened. On the and restoration of species on a thorough variables exceeded a to be guaranteed. variation on the type of role of basiphilous periodical inflow of create the presence of combined with low unique basiphilous pioneer vegetation. For primary dune fresh water, life span 0-150 years with a rich groundwater rich pioneer vegetation the Dutch Wadden selected three variables adequately sites. They were the site-specificity of with measured hydrological regimes. Two of the variables, the local drainage level (d) and the yield-factor (f), appeared to indicate sufficiently the suitability of dune slacks for basiphilous pioneer vegetation. They are, therefore, considered to be key variables representing the hydrological components of environmental control of basiphilous pioneer vegetation in dune slacks.

The oligotrophic character of natural dune slack habitats of basiphilous pioneer vegetation is generally caused by nitrogen deficiency (chapter 5). In a successional chronosequence (comprising c. 80 years) in the Koegelwieck (Terschelling), including a stage with basiphilous pioneer vegetation, nitrogen pools increased with age (chapters 4 and 6). The fairly constant annual supply of nitrogen from its main source, atmospheric deposition, corresponded to the annual storage in organic matter while net nitrogen mineralization was extremely low in all chronosequential stages. This suggested that nitrogen availability for plant growth will be almost constant during early succession. However, fertilization experiments in the Koegelwieck chronosequence showed that the type of nutrient limitation not only differs between species but also changes during early succession. Highly competitive grass species appeared to be suppressed not only by nitrogen deficiency but also by phosphorus deficiency in the earliest stages, while basiphilous species themselves only showed nitrogen limitation; they probably grow very well at extremely low phosphorus supplies. In later stages, where taller vegetation structures had developed and basiphilous pioneer species had almost completely disappeared, only species dominating the top layer of the vegetation still showed some nitrogen limitation. The other species did not show any nutrient limitation. Some of the disappearing, or less vital, species in this stage were probably outcompeted by taller species in the struggle for light.

The above results suggest that control of basiphilous pioneer vegetation at the habitat level is not only governed by a low availability of nitrogen but also by a low availability of phosphorus. The negative effects of CaCO₃ addition on the productivity of phosphorus-limited species (grasses and dwarf shrubs dominating the later successional stages in the Koegelwieck) probably indicated the most important operational effects of any buffer mechanism: fixation of inorganic phosphorus in mineral phosphates. The almost complete absence of phosphorus-limited species in the acidified stages of the Koegelwieck corroborates this supposition.

The importance of seed availability in restoration sites is illustrated in chapter 7. From the case study on this subject (again in the Koegelwieck chronosequence) it may be concluded that basiphilous pioneer species can still be found in the seed bank of relatively old successional stages. Seeds of pioneer species in general have a greater longevity than seeds of species dominating older successional stages. An estimate of longevity could only be given for a few of these pioneer species: somewhere between 40 and 80 years. Basiphilous species not found in the seed bank must spread by some means of diaspore dispersal. The tussock sedge Schoenus nigricans, not only a character species of basiphilous dune slack vegetation but also possibly facilitating the establishment and growth of other basiphilous species, apparently spreads by water
dispersal of its seeds during winter inundation. This, of course, is only possible when some tussocks are present in the close vicinity of newly developing pioneer stands. In conclusion, dispersule availability is an important factor for the development of basophilous pioneer vegetation in suitable habitats.

Conclusions on environmental control of basophilous pioneer vegetation may depend on the successional stage under study. In the earliest stage of the Koegelwieck chronosequence there were large annual fluctuations in vegetation composition while no directional changes were identified. In the most optimal stage (with most character species) on the contrary, annual fluctuations were small while directional changes, indicating a gradual development to succeeding communities, were obvious (chapter 8). It was also observed that species “at the edge of the characteristic community” fluctuated much more in response to differences in weather conditions than characteristic species.

Ways to use the key variables, identified in the present work, for decision making in the design and execution of restoration projects, are described in chapter 9. On the basis of the present investigations, combined with some general considerations, it is concluded that on the Wadden Sea islands priority should be given to restoration projects involving secondary dune slacks, especially those which are fed by calcareous groundwater from relatively large hydrological systems. Dune slack research for the use of nature restoration and management should give priority to: (i) the identification of specific threshold values of the new hydrological key variables for different basophilous plant communities and the incorporation of these variables in hydrological modelling, (ii) investigating the role of diaspore availability and dispersal mechanisms in the establishment of basophilous pioneer species in young dune slacks, (iii) assessing the relationships between geomorphological patterns and processes and the occurrence of basophilous pioneer communities in areas where water and wind driven dynamics have (re-)established.