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Development of eco-hydrological guidelines for dune habitats – Phase 1

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Development of eco-hydrological guidelines for dune habitats – Phase 1

A.J. Davy[1], A.P. Grootjans[2], K. Hiscock[3] and J. Petersen[4]

[1]Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ
[2]Community and Conservation Ecology Group (COCON), University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands
[3]School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ
[4]Nature-Consult, Fachbüro für Vegetationsökologie, Hydrogeologie und Naturschutz-Management, Hackelbrink 21, D-31139 Hildesheim, Germany

Cyngor Cefn Gwlad Cymru
Countryside Council for Wales

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Cover note

Project officer	Julie McNish, Humber to Pennines Team Julie.mcnish@english-nature.org.uk
Contractor(s) (where appropriate)	A.J. Davy Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ. A.P. Grootjans Community and Conservation Ecology Group (COCON), University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands K. Hiscock School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ J. Petersen Nature-Consult, Fachbüro für Vegetationsökologie, Hydrogeologie und Naturschutz-Management, Hackelbrink 21, D-31139 Hildesheim, Germany

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Executive summary

Wet dune slacks are distinctive wetlands that are sensitive to human influences on their hydrology. The EU Habitats Directive requires competent authorities to assess all plans and projects that could affect the nature conservation objectives of European sites (SACs and SPAs), in order to maintain their ecological integrity. The Environment Agency, as a ‘competent authority’, is responsible for reviewing all its existing authorisations, consents, licences and permissions that may significantly affect European sites in England and Wales. English Nature, the Countryside Council of Wales and the Environment Agency have collaborated to address the requirement for scientifically robust information on the eco-hydrology of wetland sites. The current project focuses on dune habitats that are sensitive to water abstraction (NVC types SD13 - SD17; European habitat features 2170 and 2190).

The aim of the project was to evaluate scientific knowledge of dune-slack habitats and provide a robust foundation for further work. The specific objectives were to:

- review relevant information on the water resource and nutrient requirements of dune-slack habitats and species;
- critically evaluate this information in order to identify significant gaps in knowledge and requirements for further work;
- provide interim recommendations for ecological target setting.

Dune slacks are characterized by seasonally fluctuating water tables; they may be waterlogged or have standing water in winter/spring but soils can dry out to a considerable depth in summer, depending on local hydrology. They must be considered as part of a larger dune system that functions as an eco-hydrological unit. The first part of the report reviews current understanding of the interactions between vegetational succession, sand buffering capacity (calcium carbonate content) and hydrology. As there has been relatively little scientific work in Britain, the review draws heavily on extensive work carried out in the Wadden Sea area, along the coasts of The Netherlands, Germany and Denmark. Successional mechanisms involve responses of different species to anaerobic conditions, acidification and nutrient enrichment, as well as the behaviour of their seed banks. The range of human impacts on dune slacks is considered, along with approaches to the restoration of their ecological function and rare species. Annex II and Red Data Book species are mainly associated with particularly sensitive early-successional stages that are base-rich and nutrient-poor.

The second part of the report concentrates on critical evaluation and the identification of research needs. Information on the hydrological conditions in a range of European dune slack habitats is used to develop a new conceptual model for dune-slack hydrology, based on a water balance approach. As it accommodates the complexity of a sequence of hydrologically connected slacks within a dune system, it does not correspond directly with WETMEC types described in previous studies in this series. Our conceptual model can, however, be used to assess the hydrological sensitivity and hydrochemical consequences of, for example, groundwater abstraction. Field measurements and quantitative modelling studies in Britain are required to validate this model and refine its predictive capability. Extensive, regular monitoring of water tables in dune slacks in England and Wales, as is carried out by Nature

Conservation staff the Netherlands, will be necessary to define the requirements of dune slack species for particular water regimes.

The report also evaluates British dune systems in the context of the geomorphological, hydrochemical and vegetational frameworks of the Wadden Sea area. There is little reason to believe that ideas developed on the Wadden coast cannot be extrapolated to the dune systems in England and Wales. The differences between them are mainly associated with the much less extensive nature of British systems. The British systems also appear to lack certain successional stages and variants (cf. Appendix 1) but this is at least partly due to limited research effort. More information is required on the vegetation and hydrochemistry of the whole range of British dune slacks to resolve this. Evaluation of Dutch restoration projects indicates that success has been limited at sites where significant degradation has occurred.

Extrapolating experience from the Netherlands (cf. Appendix 2) suggests that dune slacks may be irreversibly sensitive to water abstraction, recharge variation and changes in water quality. Recommended interim targets would be for minimal impact until the small area of British dune slacks is much better understood.

A comprehensive bibliography, including references in the text, and a list of current workers are provided.

Key words: dune slack, eco-hydrology, hydrological model, management, succession

Contents

Acknowledgements
Executive summary

1 Introduction

Dune slack habitats, like more widely distributed and better-known wetlands, are sensitive to human influences on their hydrology. The EU Habitats Directive now requires competent authorities to assess all plans and projects that could affect the nature conservation objectives of European sites (SACs and SPAs), in order to maintain their ecological integrity. Consequently, the competent authorities need a clear understanding of the potential effects of human activities on the habitats and the species for which sites were designated. Prediction of these effects is a prerequisite for weighing the likely outcomes of consented activities against appropriate ecological targets for sites and species. The Environment Agency, as a 'competent authority', is responsible for reviewing all its existing authorisations, consents, licenses and permissions that may significantly affect European sites in England and Wales.

English Nature, the Countryside Council of Wales and the Environment Agency have collaborated to address the requirement for scientifically robust information on the eco-hydrology of wetland sites (2003). Recent habitat-oriented projects have examined swamp, fen and bog habitats (Wheeler and Shaw 2000; 2001; Wheeler and others 2004), wet grasslands (Entec 2003), wet heaths (Mountford and others 2005) and wet woodlands (Barsoum and others 2005). The current project focuses on the impact of water resource and nutrient regimes on the component NVC types of Habitats Directive Annex I dune habitats that are sensitive to water abstraction. These comprise European habitat feature 2190 'Humid dune slacks' (corresponding NVC types SD13, SD14, SD15, SD16 and SD17) and European habitat feature 2170 'Dunes with *Salix repens* ssp. *argentea,* or Salicion arenariae' (corresponding NVC type SD16) (see European Commission, 2003).

The overall aim of the work was evaluate existing information on these dune-slack habitats and provide a robust foundation for further work. The specific objectives were to:

- Review relevant information on the water resource and nutrient requirements of dune-slack habitats and species
- Critically evaluate this information in order to identify significant gaps in knowledge and requirements for further work
- Provide interim recommendations for ecological target setting.

2 Methodology

This review drew substantially on research data, bibliographic databases, symposium proceedings, dissertations and reprints from journals held by the authors. This information was supplemented by reference to materials supplied by English Nature (EN; at Norwich and Peterborough), the Countryside Council for Wales (CCW), the Environment Agency (EA) and the University of East Anglia Library. Use was also made of electronic databases available at the University of East Anglia, in particular the *ISI Web of Knowledge* and the Elsevier *Scopus* system. Direct enquiries were made by email and telephone to regional staff of EN, CCW and EA, as well as to various scientific specialists.

3 Review of current scientific understanding

3.1 Introduction

Slacks are damp or wet hollows left between dunes, where the groundwater reaches or approaches the surface of the sand (Tansley 1949). One of their most distinctive features is a seasonally fluctuating water table, which usually reaches a maximum in winter and spring, and drops in summer. Two types of dune slacks can be distinguished on the basis of their geomorphological history: primary and secondary slacks (Boorman and others 1997). Primary slacks originate from sandy beaches, which have been partially or fully cut off from the influence of the sea by new foredunes, particularly in prograding systems. Exceptionally, slacks may also form from salt marshes, as dune sand encroaches on them, in for example Lincolnshire and Norfolk (G. Weaver, personal communication). Secondary slacks result from blowouts or the landward movement of dune ridges in eroding systems.

Commonly the sand is initially calcareous (from the input of shelly materials) and the groundwater is more or less base-rich, although a range of more acidic systems does also develop. As in dunes generally, the nutrient availability (particularly nitrogen and phosphorus) in pristine systems is low and this is undoubtedly one of the keys to their species diversity (Willis 1985a). Slacks are often part of the dynamic mosaic of dune habitats in time as well as space, being subject both to internal successional processes and the movements of the surrounding dunes (Ranwell 1960a). In the dynamic, successional setting of most sand-dune systems, the characteristic slack communities are maintained at least partly by disturbances, including fluctuations in the water table, blown sand, the effects of nutrient limitation and grazing. Although there has been sustained interest in the ecology and management of sand dune systems (Ranwell 1972; Ranwell and Boar 1986; Radley 1994; Packham and Willis 1997; Martínez and Psuty 2004) the slacks have tended to be neglected, especially in Britain.

In a coarsely textured, porous substrate such as sand, the depth of the dune water table has immediate consequences for plants. The amount of water that can be held against gravity is much lower than in more finely textured soils; freshly blown sand retains about 28% by mass (Willis 1985a) and even where there has been substantial incorporation of organic matter, as in the surface layers of old slacks, the value is only about 50% (Ranwell 1972). Measurements at Newborough Warren showed that sand remains saturated 10-15 cm above the free water table and capillary action carries substantial amounts of water up to 45 cm above it (Ranwell 1959). The water table has little influence on the moisture content of sand 1 m above it. Dune plants often have extensive root systems (Salisbury 1952) and may exploit water reserves at depth. Shallow-rooted plants and bryophyes are susceptible to drought as the water table drops in summer. In contrast, flooding leads to soil anaerobiosis and chemically reducing conditions in the rooting zone; the resulting toxicities can lead to the death of root systems in those species without appropriate adaptations. Paradoxically, waterlogging can produce the symptoms of drought through its deleterious effects on root function. Drought and waterlogging are opposing selective forces acting on plant species, and their alternation represents a powerful disturbance to communities. The depth and duration of winter flooding, and the severity of summer drought, are likely to be important determinants of slack community structure. The aeration associated with periodic drying also tends to promote decomposition and thus slows the successional accumulation of peat.

The water tables of moderately large dune systems have usually been reported as dome-shaped. Measurements in dip wells over an 800-ha system at Braunton Burrows, north Devon, showed that the water table was 6 - 7 m higher in the centre than near the shore line or at the inland boundary drain (Willis and others 1959a). The height of the water table was directly related to rainfall, with greater seasonal change near the centre of the dome than at the edges. Similar domes have been observed at Newborough Warren (Ranwell 1959) and Berrow, Somerset (Willis 1985a). The zone of the latter system that abuts on to a salt marsh was found to be well buffered against changes in its water level (Willis 1985a), whereas at Blakeney Point, Norfolk, where the dunes have developed on a shingle base, the tidal cycle has a marked effect on the level of the fresh water table in the dunes (Hill and Hanley 1914). More recently there has been a 20-year study of the hydrology of Ainsdale sand dunes, Lancashire, using a network of 11 groundwater observation wells (Clarke 1980; Clarke and Pegg 1993). This led to the conclusion that the levels of standing water were almost totally dependent on the effective rainfall in the preceding months.

Dune slack plant communities are typically very diverse, frequently comprising more than 100 species (Boorman and others 1997; Rodwell 2000). The number of species in a slack has been shown to be correlated with slack area (Smith 2006a). Some of these species are restricted to such coastal areas; however, dune slacks have rather few endemic species (van der Maarel and van der Maarel-Versluys 1996), and many typical dune slack species can also occur in calcareous fens, fen meadows, and other types of inland wetland. Humid slacks are refuges for certain ‘flagship’ endangered species: in Britain these include the Natterjack toad *Bufo calamita*, the fen orchid *Liparis loeselii* var. *ovata* and the thalloid liverwort *Petallophyllum ralfsii*. All of the above species are listed in either Annex II or Annex IV of the Habitats Directive and as such are the subject of conservation measures set out in the Directive. They also have many other rare species that are of conservation importance, notably *Equisetum variegatum*, *Pyrola rotundifolia*, *Moerkia hibernica* and *Dactylorhiza praetermissa* and *D. purpurella*.

Historically, the integrity and biodiversity of British dune systems have been better maintained than many other habitats, perhaps because they are often relatively remote and usually unsuitable for intensive agriculture or industrial development. They have, however, been popular areas for recreation (especially holiday tourism and golf courses). In NW Europe generally they face larger-scale threats: they have been used for abstraction of drinking water for large cities (Dutch mainland coast), experience increasing atmospheric nitrogen deposition from industrial and agricultural activities, and have been subject to large-scale afforestation (van Dijk and Grootjans 1993). In the Netherlands, where they are regarded as some of the last remnants of natural ecosystems, active restoration projects have been initiated to restore dune ecosystems to high biodiversity (Grootjans and others 2002).

3.2 British humid dune-slack communities

The composition of the NVC plant communities that correspond to Annex I humid dune slack habitat types is summarized in Table 3.1. More details of floristic composition and subtypes are given in Appendix 1 and European Commission (2003).

Table 3.1. NVC classification of wet dune communities and their more significant species After Rodwell (2000).

NVC	**NVC Name**	**Constant species**	**Rare species**
SD13	*Sagina nodosa-Bryum pseudotriquetrum* dune-slack community	*Carex arenaria, Juncus articulatus, Leontodon hispidus, Sagina nodosa, Salix repens, Aneura pinguis, Bryum pseudotriquetrum*	*Equiseteum variegatum, Pyrola rotundifolia, Moerkia hibernica, Petalopyllum ralfsii*
SD14	*Salix repens-Campylium stellatum* dune slack community	*Agrostis stolonifera, Carex flacca, Epipactis palustris, Equisetum variegatum, Hydrocotyle vulgaris, Mentha aquatica, Salix repens, Calliergon cuspidatum, Campylium stellatum*	*Dactylorhiza praetermissa, D. purpurella, Juncus acutus,Liparis loeselii* var. *ovata, Pyrola rotundifolia*
SD15	*Salix repens-Calliergon cuspidatum* dune-slack community	*Hydrocotyle vulgaris, Mentha aquatica, Salix repens, Calliergon cuspidatum*	
SD16	*Salix repens-Holcus lanatus* dune-slack community	*Carex flacca, Festuca rubra, Holcus lanatus, Lotus corniculatus, Salix repens*	
SD17	*Potentilla anserina-Carex nigra* dune-slack community	*Agrostis stolonifera, Carex nigra, Potentilla anserina, Calliergon cuspidatum*	

Information on the successional characteristics and eco-hydrological requirements of these five communities and their subtypes tends to be anecdotal, being derived usually from rather few sites:

3.2.1 SD 13: *Sagina nodosa-Bryum pseudotriquetrum* dune-slack community

This is generally regarded as a pioneer or immature community of drier slacks between stabilized, calcareous dunes. These slacks are moist in winter and dry at the surface in summer (Rodwell 2000). Successional development is arrested and renewed by disturbance, particularly the periodic shallow submergence. Grazing by rabbits and stock, or summer drought may also be factors in keeping the vegetation low and open. Winter flooding is typically to a depth of c. 2 cm and the summer water table varies 60-160 cm below the surface (Willis and others 1959b; Hope-Simpson and Yemm 1979).

3.2.2 SD14: *Salix repens-Campylium stellatum* dune slack community

These communities form in moderately wet, highly calcareous slacks, where there is a large range of water table level and base-rich groundwater (Rodwell 2000). Winter flooding may reach a depth of 10-50 cm and the summer water table may be 10-60 cm below the surface (Gorham 1961; Willis and Yemm 1961; Willis 1963; Jones 1993a).

3.2.3 SD15: Salix repens-Calliergon cuspidatum dune-slack community

This is characteristic of older slacks with prolonged flooding, for up to 8 months per year. However, the level of the water table varies relatively little: flooding is less than 5 cm above the surface and the water table only drops to 40 cm below the surface (Willis and others 1959b; Jones 1993a). Vascular plants are unlikely to experience drought under this regime but bryophytes might.

3.2.4 SD16: *Salix repens-Holcus lanatus* dune-slack community

This is the vegetation of older slacks that are only rarely and transiently flooded. The water table is typically 50-200 cm below the surface in summer (Ranwell 1972; Jones 1993a). As flooding does not represent a significant disturbance, successional development is probably inhibited by grazing of stock or rabbits.

3.2.5 SD17: *Potentilla anserina-Carex nigra* dune-slack community

These are communities of wet slacks where the groundwater is not particularly base-rich. Little is known about groundwater levels but flooding may be to a depth of 50 cm. As they are often in areas of high rainfall, periods of water shortage may be transient. They are generally associated with mature dune grasslands and stable dune ridges. Repeated flooding and grazing probably limit successional change (Rodwell 2000).

The total areas of dune slack community in Britain are remarkable small, a fact that accentuates concerns for their protection. The entire extent of all slack communities in England and Wales is slightly less than 1000 ha (Table 3.2).

3.3 Calcium carbonate content of the sand

Calcium carbonate content is crucial in determining the hydrochemistry of dune slacks and the development of their vegetation. The soils of primary slacks are usually calcareous, since they normally originate from recently deposited sands that contain abundant shell fragments. Most foredune sands on the coast of England and Wales contain at least 1% $CaCO_3$ and those on the more exposed west coasts may contain 10-50% (May 2003). Dune slacks with acid soils occur in areas where sand with low initial lime content has been deposited on the beach. Examples are such relatively acid dune areas can be found on the east coast of Britain (eg Winterton Dunes, Norfolk), along the Polish coast (Piotrowska 1988), but also in certain areas of the Dutch, German and Danish Wadden Sea Islands, where initial lime contents are low, with less than 2% $CaCO_3$, (Petersen 2000) and where precipitation dominates over evaporation. These conditions promote decalcification processes in the upper sand layer and thus rapid acidification (Stuyfzand 1993). The soil in young, primary slacks can be buffered by any combination of brackish surface water, $CaCO_3$-rich sand, and calcareous groundwater.

Table 3.2. Total areas (ha) of humid dune slack communities in England (Radley 1994) and Wales (P. Rhind, personal communication).

Community	England	Wales	Total
SD13	4.00	13.22	17.22
SD13a	0.04		0.04
SD13b	7.32	1.91	9.23
Total SD13	11.36	15.13	26.49
SD14	11.04	25.64	36.68
SD14a	9.19	0.68	9.87
SD14b	5.27	52.09	57.36
SD14c	0.41	5.59	6.00
SD14d	8.59	18.02	26.61
Total SD14	34.50	102.02	136.52
SD15	18.39	29.61	48.00
SD15a	6.25	16.92	23.17
SD15b	36.65	19.94	56.59
SD15c	7.99	19.16	27.15
SD15d	65.85	1.37	67.22
Total SD15	135.13	87.00	222.13
SD16	123.23	138.00	261.23
SD16a	15.23	5.23	20.46
SD16b	43.45	6.75	50.20
SD16c	13.35	18.82	32.17
SD16c/d		9.73	9.73
SD16d	32.33	38.40	70.73
Total SD16	227.59	216.93	444.52
SD17		19.04	19.04
SD17a	5.43	7.37	12.80
SD17b	15.29	15.12	30.41
SD17b/d		2.67	2.67
SD17c	0.04	9.96	10.00
SD17c/d		0.87	0.87
SD17d	36.92	33.65	70.57
Total SD17	57.68	88.68	146.36

Secondary slacks are also usually calcareous and they may or may not be supplied by calcareous groundwater. Either way, the vegetation may be very similar since infiltration of rainwater also leads to base-rich conditions, since $CaCO_3$ is dissolved in the rooting zone almost immediately. Surface waters from dune slacks at Sandscale in N. Lancashire were as highly calcareous as waters from limestone areas (Gorham 1961). Secondary, *in* *situ*, carbonate deposition has also been observed in dune slacks. It occurs when exfiltrating groundwater, (over)saturated with respect to calcite, enters the slack. Loss of CO_2 from this water results in carbonate precipitation at the soil-air interface (Chafetz 1994) thus counteracting soil acidification. Such carbonate precipitation can only occur when water tables remain very high during summer (c. 40 cm below the surface) and capillary rise of calcareous groundwater is possible.

3.4 Succession in dune slacks

Both the colonization of embryo slacks close to the coast and the cyclic succession of slack communities associated with mobile dune systems were described in detail at Newborough Warren, Anglesey some half a century ago (Ranwell 1960a). Embryo slacks are still affected to an extent by salinity and may be flooded by exceptionally high tides. The establishment and growth of *Salix repens* is of structural importance in a cycle of about 80 years duration. *S. repens* becomes established in wet slacks dominated by *Agrostis stolonifera* and, as accretion proceeds, dominates first wet and then dry slacks, before trapping sand into low dunes. These are typically engulfed by the passing wave of an *Ammophila* dune, or may undergo direct erosion back to low-lying, bare damp sand. Subsequent detailed ordination analysis of these dune-slack communities identified water-table depth, unsurprisingly, as correlated with the primary axis of vegetational variation, and found weak trends in calcium and sodium availability along the second axis of variation (Onyekwelu 1972a). A very similar dune-slack successional sequence occurs within the blow-outs in the highly mobile dune system at Braunton Burrows, north Devon (Willis and others 1959b). The primary colonists are algae, followed by bryophytes, *Agrostis stolonifera* and *Juncus articulatus,* and then *Salix repens*; seedlings of the latter are often zoned as a ring corresponding with floodline of the slack basin. Subsequently, more diverse vegetational variants with many characteristic dune-slack species develop, depending on the wetness of the site. A greater range of developmental relationships has been described at Tentsmuir in Scotland; they start with a salt-tolerant *Honkenya peploides-Juncus gerardi* type that evolves initially into a *Salix repens – Juncus balticus* type and later into a variety of communities, again depending on water table depth and flooding frequency (Crawford and Wishart 1966). Recently, Smith (2006a) has examined floristic changes in 26 slacks in the Birkdale Sandhills part of the Sefton Coast, Lancashire, after an interval of 20 years. Many of the changes were attributed to successional change, particularly in young slacks initiated during an exceptionally dry period in the mid-1970s.

Functionally, natural succession in dune slacks can be roughly divided into 4 phases (Figure 3.1). In the pioneer phase (phase 1) small pioneer species establish on an almost bare soil, which is usually covered with a thin layer of green algae and laminated microbial mats (van Gemerden 1993; Grootjans and others 1997). In phase 2, higher plants adapted to very low nutrient availability colonize. In phase 3, a moss layer of pleurocarpous bryophytes develops and typical dune slack species become established. Subsequently (phase 4) there can be rapid accumulation of organic matter and increase of tall grasses and shrubs appears, which leads to the decline of typical dune slack species.

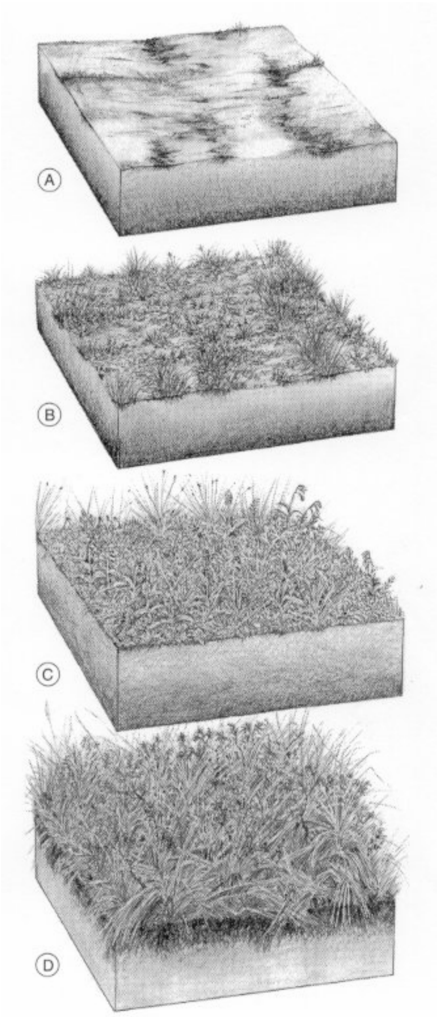

Figure 3 1. Vegetation development in a wet dune slack starting as sparsely vegetated pioneer stages (a and b), proceeding to a stage with many Red List species (c), until tall grasses and shrubs take over (drawing by Rob Beentjes).

The microbial mat in phase 1 stabilises the sandy substrate (Pluis and de Winder 1990). The Cyanobacteria in the microbial mats can fix nitrogen (Stal and others 1994) and may, therefore, assist in the colonisation by higher plants. Red list species, such as *Liparis loeselii, Dactylorhiza incarnata* and *Epipactis palustris* are most abundant in phase 3. However, the dense layer of pleurocarpous bryophytes in this phase promotes the rapid built up of organic material and the establishment of tall grass and willow species. The shift from pioneer stage to more mature stages usually takes place 20-30 years (van der Maarel and others 1985). In some dune slacks, however, pioneer stages may persist for at least 30-60 years (Petersen 2000; Adema and others 2002).

The direct monitoring of factors governing vegetation succession over a period of more than half a century is rather impracticable. However, sod-cutting experiments, in which the organic top layer is removed, are available in some dune slacks, where nature managers have tried to restore pioneer stages at various times. Such a spatial representation of supposed successional stages is called a chronosequence. An analysis of vegetation development in one chronosequence (Berendse and others 1998) showed that during the first 10 years most of the organic matter was stored in the living plants, particularly in the root system (Figure 3.2). After about 15 years the amount of soil organic matter increased, while the pH dropped steeply, and a thick (c. 10cm) organic layer developed. This drop in pH only occurred in dune slacks which were poor in $CaCO_3$, and did not occur in sands with lime contents more than 0.3 % $CaCO_3$ (Ernst and others 1996).

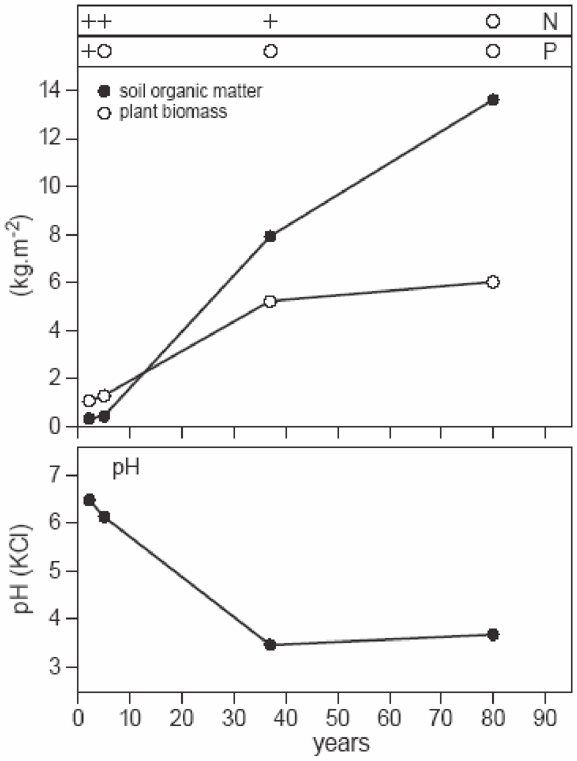

Figure 3.2 Plant biomass, soil organic matter and soil pH measured in a chronosequence on the Dutch Wadden Sea island of Terschelling, representing various succession stages (2, 5, 37, and 80 years). Responses of the plant biomass to the addition of nitrogen and phosphorus fertilizer (16g m^{-2}) are indicated above (Berendse and others 1998).

Early fertilization experiments at Braunton Burrows (Willis 1963) showed that diverse wet-slack vegetation was severely limited by nitrogen and phosphorus supply; when complete nutrients were added, *Agrostis stolonifera* rapidly predominated, with an increase in vegetation height of up to 15-fold, and the loss of many of the distinctive slack species. Fertilisation experiments in different chronosequential stages (that originated from sod cutting at different time intervals) in Wadden Sea slacks showed that late successional grass species, such as *Calamagrostis epigejos* and *Agrostis stolonifera*, are already present in pioneer stages, but that their growth was limited by a low availability of both nitrogen and phosphorus (Ernst and others 1996; Lammerts and others 1999). The pioneer species of low productivity, in particular *Juncus* and *Carex* species, were limited only by nitrogen (Lammerts and Grootjans 1997), probably because they have a very low phosphorus demand (Willis and Yemm 1961; Willis 1963; van Beckhoven 1995) *Schoenus nigricans* showed no response at all to either nitrogen or phosphorus additions. This implies that, as long as phosphorus limits the growth of tall grasses, a basiphilous pioneer vegetation can persist for quite some time, even when nitrogen availability increases. Buffer mechanisms that keep the soil pH above 6, appear to be crucial for maintaining a low phosphorus availability. Adding lime in the fertilisation experiments had the same effect on biomass production as the effects of co-limitation by nitrogen and phosphorus. Phosphorus availability is relatively high in older and acid stages in dune slacks of the Dutch Wadden Sea islands because the soils are poor in iron here and the phosphorus is, therefore, only loosely bound to iron-organic compounds (Kooijman and Besse 2002). Tall-growing, late successional grass species, such as *Calamagrostis epigejos*, rapidly increase in cover after nitrogen and phosphorus limitations have been relieved (Ernst and others 1996).

Atmospheric input of nitrogen may accelerate the accumulation of organic matter in the topsoil considerably, because the growth of most pioneer and mid-successional species is N-limited and therefore, responsive to additional supply of nitrogen. (Jones and others 2002b) have made a detailed review of the consequences of changing nutrient budgets of dunes for their conservation interest and management. They provide a critical assessment of the use and limitations of the Ellenberg 'Indicator' ordinal scales. The Ellenberg scores for individual species have been used to characterize their communities and predict their sensitivity and responses to eutrophication. Application of the Ellenberg nitrogen indicator led to the conclusion that the dune-slack communities SD13, SD14, SD15, SD16 and SD17 were considered to be most at risk from eutrophication, not just because of their low mean scores but also because nitrogen leached from the surrounding dunes would be likely to accumulate in groundwater.

British dune sands, such as Kenfig Burrows, may be relatively iron- and manganese-rich. As in other wetlands (Armstrong 1975; Snowden and Wheeler 1993), the anoxic conditions concomitant with waterlogging in dune-slack soils result in lower redox potentials (Jones and Etherington 1971) and increased solubility of Fe and Mn, especially during the prolonged winter-spring flooded period and where there is more organic matter in the soil (Jones 1973). An experimental comparison of important dune-slack grasses (*Agrostis stolonifera*, especially *Festuca rubra*) and sedges (*Carex flacca* and *C. nigra*) showed tolerances that were consistent with their field successional and topographic distributions. The grasses, especially *F. rubra*, were more adversely affected by waterlogging (Jones and Etherington 1971) than the sedges. *A. stolonifera, C. flacca, C. nigra* took up more Fe and Mn when experimentally waterlogged, and more from a slack sand with higher organic content; plants of all species collected from wetter sites also contained more of these metals (Jones 1972a). High Mn concentrations induced toxicity symptoms in *F. rubra* (and to a lesser extent in *C. nigra*) but *A. stolonifera* was unaffected (Jones 1972b). *A. stolonifera* and *F. rubra* showed reduced phosphorus contents under waterlogging, probably because of immobilization of soil phosphorus by iron; however, *C. flacca* and *C. nigra* had increased P contents (Jones 1975b). The shoot content of potassium was not influenced by waterlogging but that of roots was depressed in all four species (Jones 1975a).

3.5 Seed banks and succession

Seed bank research (Bekker and others 1999) has shown that most pioneer species, such as *Centaurium pulchellum*, and several *Juncus* species have long-term persistent seed banks and that many late successional species, such as *Salix repens, Eupatorium cannabinum* and *Calamagrostis epigejos* have transient seed banks (Thompson and others 1997). An extreme example is *Salix repens*, whose seeds do not survive storage for more than a month (Ranwell 1960a). The species that had long term-persistent seed banks were also those that appeared immediately after sod cutting, even if the original pioneer vegetation had disappeared several decades previously. Fig 3.3 clearly shows that the group of dune slack pioneer species as a whole had long-term persistent seed banks with seeds surviving at least 5 years but often for longer periods.

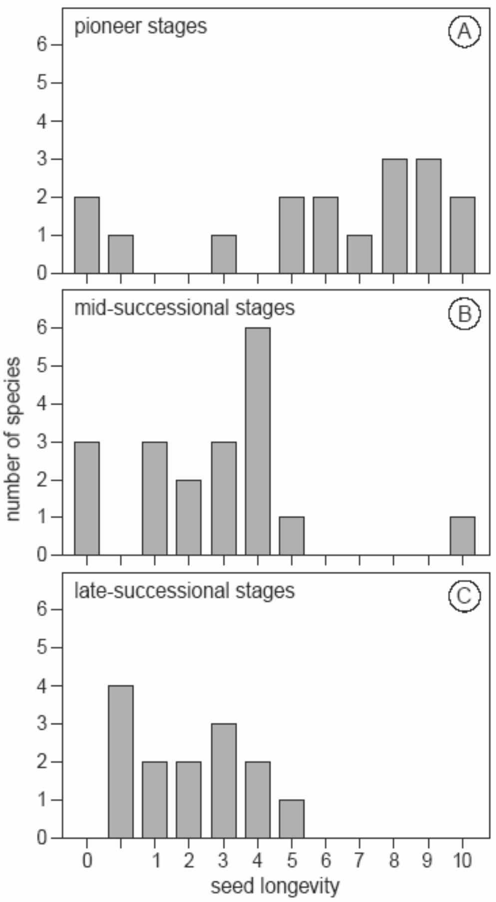

Figure 3.3 Seed longevity of dune slack species of (a) pioneer stages, (b) mid-successional stages, and (c) late-successional stages (Bekker and others 1998).

The longevity index in Figure 3.3 (Bekker and others 1998) has been constructed from records of longevity in the database of (Thompson and others 1997). It indicates the 'average' period of seed survival in the soil. An index of 0-3 means that the seeds are transient; they cannot survive in the soil longer than one year. The range 4-7 indicates that seeds can survive for 1–5 years, and from 8-10 seeds survive for more than 5 years. The group of late successional species had short-lived or transient seed banks, while the seed longevity of the group of mid-successional species was intermediate. However no data are available with respect to many typical dune slack species, such as orchid species, which are critically endangered in NW Europe. This means that we cannot necessarily rely on the persistence of living seeds in sites where these species used to be found and have disappeared recently during vegetation succession.

3.6 Hydrological conditions and the rate of succession

Most dune slacks are fed by various water sources. These can be precipitation water, surface water or groundwater. The latter two sources are usually calcareous while the former is acid. The hydrological situation can be more complicated (see section 4.1), since the groundwater may come from different hydrological systems (Munoz-Reinoso 2001b; Grootjans and others 2002). In most cases the maintenance of dune slack ecosystems depends on both the amount of precipitation and groundwater discharge. Dune slacks fed by calcareous groundwater are usually situated at the low-lying periphery of the dune system, where most of the groundwater of the main hydrological system discharges. However, seepage slacks can also be found close to the top of the main hydrological system when thick clay or peat layers impede infiltration to deeper layers and give rise to perched water table conditions and local groundwater flow towards adjoining dune slacks. Such slacks function as 'flow-through lakes' with groundwater discharge in one part of the slack and infiltration of surface water in another (Stuyfzand 1993). In a dune area with several dune slacks lying close together, slight differences in water level between the slack may initiate groundwater flow from one slack to another (Kennoyer and Anderson 1989; Grootjans and others 1996). Under such conditions calcareous groundwater from deeper layers can flow towards the up-gradient parts of the slack. The influx of calcareous groundwater stimulates mineralization of organic matter and consequently the successional accumulation of organic matter is lower under its influence than at the infiltration sites (Sival and Grootjans 1996).

Pioneer stages were found to be much more persistent in groundwater-fed dune slacks than those situated in infiltration areas (Lammerts and others 1995). The algal/microbial mats characteristic of early succession stages lead to the productions of toxic sulpide ions, as sulphate is used as an electron acceptor by photosynthetic autotrophs under anaerobic conditions. Oxygen penetration in microbial mats is shallow ranging from less than 2 mm depth in the dark to 5-6 mm during active photosynthesis (van Gemerden 1993). Anoxic, iron-rich groundwaters have a large capacity to immobilize sulphide but the iron-depleted sands of infiltration sites release phosphates when exposed to sulphide, which can accelerate succession (Lammerts and others 1999). The additional nitrogen fixed by cyanobacteria in microbial mats (Stal and others 1994) may also assist in colonisation by higher pants. Thus, factors which stabilise the longevity of the pioneer stages that support many Red List species may always be associated with a regular supply of groundwater. These important hydrochemical issues are considered on more detail in section 4.4.

3.7 The impacts of human disturbance

Episodes of high dune-slack biodiversity are often associated with disturbance and thus mark the beginning of a recovery process after a period of over-exploitation of the dune environment. World War II represented such a period in the Wadden Sea area. Sod cutting in the slacks occurred frequently but there is little documentation as to why: fertilisation of gardens and roofing materials have been mentioned (Beinker 1996) but no real historical evidence has been presented. One clear reason for the sod-cutting appears to have been for material to cover the fortifications of the German Atlantic Wall. These activities had a valuable side-effect: dune slack succession was set back on a large scale and this is one of reasons why many pioneer and typical dune slack species can still be found along the NW-European coast.

Factors that have contributed to the subsequent dramatic decline of biodiversity in wet dune during the second half of the 20th century include lowering of the water levels in the adjacent polder areas, reclamation for agricultural use and afforestation with pine plantations. In the Netherlands, large scale disturbances of dune slack environment started as early as 1853, when the vast stock of fresh dune water became a major source of drinking water production for the large cities; large dune areas actually became drinking water catchments. This exploitation resulted in a large-scale lowering of the water table by 2-3 m on average (Bakker and Stuyfzand 1993). At the same time large parts of the dune area were preserved as a landscape in a time of rapid industrialisation and rapid urbanisation in this densely populated area.

Munoz-Reinoso (2001b) has reported on similar negative effects of groundwater abstraction in the Doñana National Park in Spain. The impact of a groundwater abstraction facility near a large tourist resort was obscured by large fluctuations in precipitation from year to year. Aerial photographs indicated a clear increase of scrub and trees (notably *Pinus pinea* from surrounding pine plantations) along the shores of dune ponds over a period of 23 years. He suggested the following mechanism for the spread of trees. The invasion of trees and large shrubs is prevented under natural conditions by the occurrence of exceptionally high floods during the spring, which kill most of the species from drier habitats. This flooding frequency stabilises the open grassy and heath vegetation that is adapted to temporarily very wet conditions. The abstraction of groundwater from the main aquifer prevents some discharge of groundwater in the dune ponds, thus preventing the exceptional high floods even in areas situated more than 5 km away (González Bernáldez and others 1993).

In Britain coastal dunes have been prime sites for the development of golf courses (‘links’). The effects of this have inevitably been wider than just on the area used for play because water is often abstracted from the dune system to irrigate the greens. Artificial lowering of the water table by this or other forms of drainage is bound to affect the communities of the dune slacks, as has been shown by the Dutch work. This water abstraction, however, occurs locally and has never been a problem on the scale experienced by Dutch dune systems (Jones 1993b). Historically, partial afforestation (mainly with pine species) has been a feature of many nationally important dune systems (including Ainsdale, Newborough Warren, Holkham and Tentsmuir). Originally it was for shelter and timber crops but more recent plantings have been for amenity use and even conservation (Edmondson and others 1993). The water interception and transpiration associated with forest is likely to be an adverse influence groundwater recharge and levels (Betson and others 2002; Bristow 2003).

The very negative effects of drinking water extraction in the Dutch dune areas led to the development of new production techniques. To raise the water tables in the dried-out dune areas, surface water from the rivers Rhine and Meuse was transported into the dunes and was infiltrated in the soil through an extensive network of ponds and canals. For nature conservation this technique was disastrous. The input of polluted river water led to increased water tables in the dune slacks, but at the same time promoted eutrophication in practically all dune slacks (van Dijk and Grootjans 1993).

In Dutch dune areas less affected by this, such as the Wadden Sea coast, 70 years of dune fixation, in which every spot of bare soil had to be covered with branches or hay, by law, resulted in an almost complete stop in natural dune formation. This has led to rapid vegetation succession not only in dry dunes, but also in slacks. For economic reasons grazing by cattle has stopped in most of European coastal areas. This has led to enhanced grass encroachment (Veer 1997) and the development of woodland. A positive feedback mechanism exists between increased biomass production and decreased groundwater levels. Tall vegetation types, such as shrubs and forests intercept more nutrients from atmospheric deposition than relatively open and short vegetation types, leading to increased growth and a higher evapotranspiration. The result is further reduction in water tables during the summer and consequently in a decreased discharge of groundwater in the dune slacks (Stuyfzand 1993). If the supply of groundwater decreases, shrubs and tall grass species invade the site and pioneer communities are lost to competition.

The succession has been stimulated even more by increased atmospheric N-deposition during the last 50 years. The total amount of nitrogen which has been deposited on the vegetation via precipitation and dust particles increased from c. 10 kg N ha^{-1} yr^{-1} in 1930 to c. 25 kg N ha^{-1} yr^{-1} in 1980 (Stuyfzand 1993) and has stabilised between 25 and 35 kg N ha^{-1} yr^{-1} in the late 90's (ten Harkel and van der Meulen 1996; van Wijnen 1999). Nitrogen deposition is a particular concern for British Dune systems. A large-scale survey indicated that evidence of change as a result of atmospheric deposition is less clear in slacks than on dry dune habitats (Jones and others 2002a; Jones and others 2004), although *Carex arenaria* and *Hypochaeris radicata* may be increasing in slacks. However, N deposition is bound to find its way into groundwater. Jones and others (2002a; Jones and others 2004) suggest a critical load range of 10-12 kg N ha^{-1} yr^{-1} for coastal sand dunes in the UK. Similarly, an intensive study of the nitrogen budget of Merthyr Mawr dune system did not find discernible effects of NH_3 deposition on slack habitats but could identify local sources of eutrophic groundwater (Jones and others 2005). The potential complexities of such analysis are illustrated by the fact that summer and winter groundwater levels were influenced not only by rainfall but also by multiple groundwater feeds with several months' lag.

3.8 Management techniques to conserve dune slack vegetation

A variety of methods has been used to promote disturbance and set back succession.

3.8.1 Mowing

Mowing is a traditional management technique, which when applied without addition of fertiliser or manure, prevents grasses, willows (*Salix*) and tree species from dominating the vegetation, thus favouring many non-competitive Red List species. The production of dead biomass is reduced because part of the biomass is harvested. This leads to decreased nutrient cycling within the ecosystem and might even lead to a shift in the type of nutrient limitation (Koerselman 1992; Verhoeven and others 1996). Mowing does not prevent the accumulation of organic matter in the top layer and it does not prevent acidification in decalcified soils. Mowing, therefore, is most efficient in sustaining basiphilous pioneer stages in areas where the soil is well buffered against acidification and where nutrient cycling is still low; in calcareous dune soils and in soils with a strong discharge of calcareous groundwater. Mowing early in the season can be very harmful, because it affects reallocation of nutrients in *Schoenus* tussocks and prevents seed set.

3.8.2 Grazing

Grazing is often applied in dry dune to combat grass and shrub encroachment. In wet dune slacks, cattle and horses may damage young pioneer stages by trampling and by polluting surface water. The effect of grazing by rabbits is most pronounced in early stages of succession. They may eat 40-50% of the shoot biomass during the first three years after sod cutting (unpublished data of Van der Veen). Boorman (1989) concluded from a survey of 48 British dune sites that moderate grazing by cattle was the best management for the dune slacks to maintain species diversity. Accumulation of organic matter is not prevented by grazing, but perhaps retarded, because of the lower input of litter (Kooijman and de Haan 1995). Species richness is locally stimulated by cattle grazing and some dominant species, such as *Calamagrostis epigejos*, *Salix repens* and *Carex arenaria* decrease in cover (van Dijk 1992; de Bont and others 1999)). In general grazing promotes low structured vegetation types and creates a more fine-grained vegetation pattern. In the Moksloot area (an old primary dune slack on the N.E. coast of Texel) cattle reduced tall reeds and tall sedges including rare species such as *Ranunculus lingua*, leaving a monoculture of *Iris pseudacorus*.

3.8.3 Rewetting

Currently, hydrological systems are being adapted more frequently to raise water tables in dune areas. The most obvious measure is to reduce abstraction of natural dune water. In the National Park of "Zuid Kennemerland", for instance, previous groundwater extraction of 9 Mm^3 a year has ceased. A large production canal of 2.5 km has been eliminated in the dunes near Amsterdam, leading to a spectacular rise in water tables of 2 m. Rewetting was combined with a restoration project of the whole dune landscape (Geelen and others 1995). In the near future the elimination of groundwater extraction will lead to further rewetting of hundreds of hectares of desiccated dune slacks. In the Meyendel area, a production field with surface infiltration was recently removed to restore the hydrological system. This became possible after the development of new production techniques, such as deep-well infiltration and membrane filtration (Jannson and Salman 1995). Further local plans include closing drainage ditches and hydrological isolation of lowlying polders by placing artificial barriers in the soil to prevent loss of groundwater.

In order to restore species-rich dune slacks, rewetting of desiccated slacks should be combined with one of the other management techniques. Otherwise grasses, tall herbs and shrubs soon dominate the vegetation.

3.8.4 Sod cutting

Sod cutting includes the removal of the black organic A-horizon and leaving the mineral C-horizon intact. This type of management is traditional and has been practised (manually) on most of the Dutch, German and Danish coastal dune areas for a long time (Petersen 2000). Nowadays, sod removal is often carried out with large machines and can affect sections of the mineral subsoil as well. In many restoration projects the dune slack is deliberately deepened, to promote rewetting of the slack. This approach of combining decreasing nutrient stocks with rewetting has been applied on a large scale in Dutch dune areas, but deviates from natural dune slack formation in several ways. First, large-scale sod cutting is carried out within a very short time, usually in summer, when water levels are low. Natural formation of dune slacks, however, proceeds gradually. It may take many years before a beach plain is effectively cut off from the influence of the sea by enclosing dune masses or before intensive sand blowing stops when the local water table had been reached. In this way colonisation can proceed slowly through stepwise establishment of local populations. Secondly, sod cutting removes most of the existing vegetation and may also remove relict populations of endangered plant species. For this reason parts of the mature vegetation are usually left intact.

3.8.5 Constructing and restoring slacks

New slacks have been created, for instance, when sand is needed for coastal defence in order to fill in ‘weak’ spots in the fore dunes. Dune slacks have also been created unintentionally, sometimes as a result of the creation of sand dikes, which were intended to prevent erosion by storm floods or just to reclaim land from the sea. Some of the largest and best-developed dune slacks were ‘created’ in this way on the Dutch Wadden Sea islands. Sometimes new dune slacks have been constructed to compensate for damage inflicted to dune slacks elsewhere (Londo 1971; Westhoff and van Oosten 1991).

Considerable efforts have been made in many parts of world for the restoration of coastal dune systems (Greipsson 2002), on the one hand, and freshwater wetlands (Wheeler and others 2002), on the other, but little attention has been directed to the specific hydrological conditions of dune slacks. The restoration of Dutch coastal dune slacks, including the use of all of the techniques described in section 3.8, has been reviewed in detail by Grootjans and others (2002). In Britain there is particular interest in setting-back succession by scraping new slacks, or deepening existing ones, and this may be considered reasonably successful, at least for the limited objectives of providing seasonal breeding sites for Natterjack toads (see section 3.9.1). The wider implications are not well understood and there are likely to be important site-specific considerations. Although lowering the land surface clearly can re-establish the relative water table level locally, it may not restore its amplitude of variation or produce the desired water quality; such proposals need to take account of the potentially complex hydrology and hydrochemistry of dune slacks (see section 4.1).

3.9 Rare and endangered species

3.9.1 Natterjack toad *Bufo calamita*

The natterjack toad is the rarest British amphibian and has been the subject of prolonged and substantial conservation efforts (Banks and others 1994). It has disappeared from 75% of its previously recorded habitats in the last century and occupies fewer than 50 sites today, where it breeds in mainly in ponds and ephemeral pools within dune slacks and wet heaths. The natterjack suffers strong adverse effects from inter-specific competition with commoner toads and frogs (*Bufo bufo* and *Rana temporaria*) through both resource and interference mechanisms (Bardsley and Beebee 2001).

Its decline is attributed partly to habitat destruction but mostly to successional changes in its specialized habitats and anthropogenic acidification of breeding sites. Acidic water (pH c. 4.5) increases spawn mortality and reduces tadpole growth rate (Denton and Beebee 1997). Conservation efforts have therefore focused on restoration and maintenance of early seral stages of succession (Banks and others 1994; Beebee and others 1996; Denton and others 1997). Slacks have been artificially deepened or new ‘scrapes’ made within them, for example in the Sefton Coast dunes (Smith 2006a), to provide breeding habitat.

3.9.2 Fen orchid *Liparis loeselii*

Two forms of this orchid are found in Britain: the typical fenland form is known from three locations in the Norfolk Broadland (Wheeler and others 1998) but the smaller, shorter-leaved *L. loeselii* var. *ovata* is a rare and protected plant that is confined to early or mid successional dune slacks, referable to the NVC SD14 *Salix repens-Campylium stellatum* community, at sites around the Bristol Channel but mainly in S. Wales (Jones and Etherington 1992; Jones 1998). In these slacks the water table regularly falls to more than 0.5 m below ground level during August and September. Its early successional status is reflected in the fact that in Britain it is typically found only 11-15 years after the damp, bare-sand stage, although elsewhere in Europe this interval can be longer (Jones 1998). Its regeneration in later successional stages may be inhibited by the dense mat of pleurocarpous mosses that develops. *L. loeselii* had an optimum soil pH of 7.3 in a large sample of dune slacks in the Frisian Islands (data of J. Petersen).

3.9.3 Petalwort *Petalophyllum ralfsii*

Petalwort is a thalloid liverwort that is found only in early successional or recently renewed dune slack habitats referable to the NVC SD13 community. This is a very rare community, occupying only 26.5 ha in England and Wales (Table 3.2). It is characterized by calcareous sands and shallow submergence with water in winter, combined with drying at the surface in summer. SD13 is very susceptible to any successional development, especially the growth of *Salix repens* and *Calliergon cuspidatum*, and is considered on the verge of extinction (Jones and Etherington 1989). Very little appears to be known about the autecology and requirements of *Petalophyllum*. Forms previously thought to be *Petalophyllum ralfsii* in N. America, Australia and New Zealand have recently been accorded separate specific status (Crandall-Stotler and others 2002).

4 Critical evaluation

4.1 Hydrological and hydrochemical conditions of humid dune-slacks

4.1.1 Hydrological conditions and dune-slack types

Hydrological and hydrochemical controls on humid dune-slacks are dependent on several factors including climatic setting, coastal geomorphology, hydrogeological conditions and substrate mineralogy. The hydrological regime of a dune-slack is essential for a good functioning of the dune-slack ecosystem. To demonstrate the interconnection of these controls, Figure 4.1 provides a general conceptual model showing the position of dune-slacks in a coastal zone connected to an inland area with an underlying regional aquifer or aquitard. Five types of dune-slack are shown, A, B, C, D and E. Not all types will be present at a location, for example Type D is not expected in island situations. Two groundwater flow systems are shown: a local circulation of fresh groundwater in the dune system and recharged directly by precipitation; and a regional groundwater flow system originating in the inland area and discharging in the coastal zone. The degree of influence of the regional flow system will depend on the extent and nature of the underlying geological unit as to whether it forms an aquifer of good hydraulic conductivity or an aquitard of poor hydraulic conductivity. Local groundwater flow circulation in the dune system will occur at depth if the sand is free draining with a shingle base but flow may be restricted vertically by the presence of clay lenses or peat layers.

The topographic elevation of the dune system and inland areas determines the shape of the water table. As show in Figure 4.1, the inland area and the dune system are unconfined with groundwater discharge directed towards topographic hollows. Hollows in the dunes may be formed by blow outs or as a result of successive dune formation landwards. Dune-slacks of Types B and C are fed solely by precipitation infiltrating the dune sands. In Type B, groundwater flow is directed towards the slack and water is lost by evapotranspiration. An example of Type B is shown in Figure 4.2. In Type C, groundwater flows into the up-gradient edge of the slack, flows through the slack and then exits the slack at the down-gradient edge before continuing to flow in the direction of the hydraulic gradient (Stuyfzand 1993). In a dune area with several dune-slacks lying close together, slight differences in water level between the slacks may initiate groundwater flow from one slack to another (Kennoyer and Anderson 1989; Grootjans and others 1996).

Type D is at the boundary between the dune system and inland area and is fed by both the regional and local groundwater flow systems and, as shown, may receive some surface water runoff. An example of Type D is shown in Figure 4.3. Type E represents a moist dune-slack situated at a high elevation in the main dune area. Moisture in the capillary fringe above the water table keeps the base of the dune-slack moist with only occasional flooding when the water table is high in wet years. An example of Type E is shown in Figure 4.4. The dune-slacks inland of the large fore-dune (Types B, C, D and E) are above the brackish water body in the subsurface although the seaward Type A dune-slack is in reach of the transition zone between the circulation of fresh and saline groundwaters and so may be subject to brackish conditions. Dune-slack A is in the most dynamic part of the coastal environment and is considered only temporary as the developing dune system moves inland.

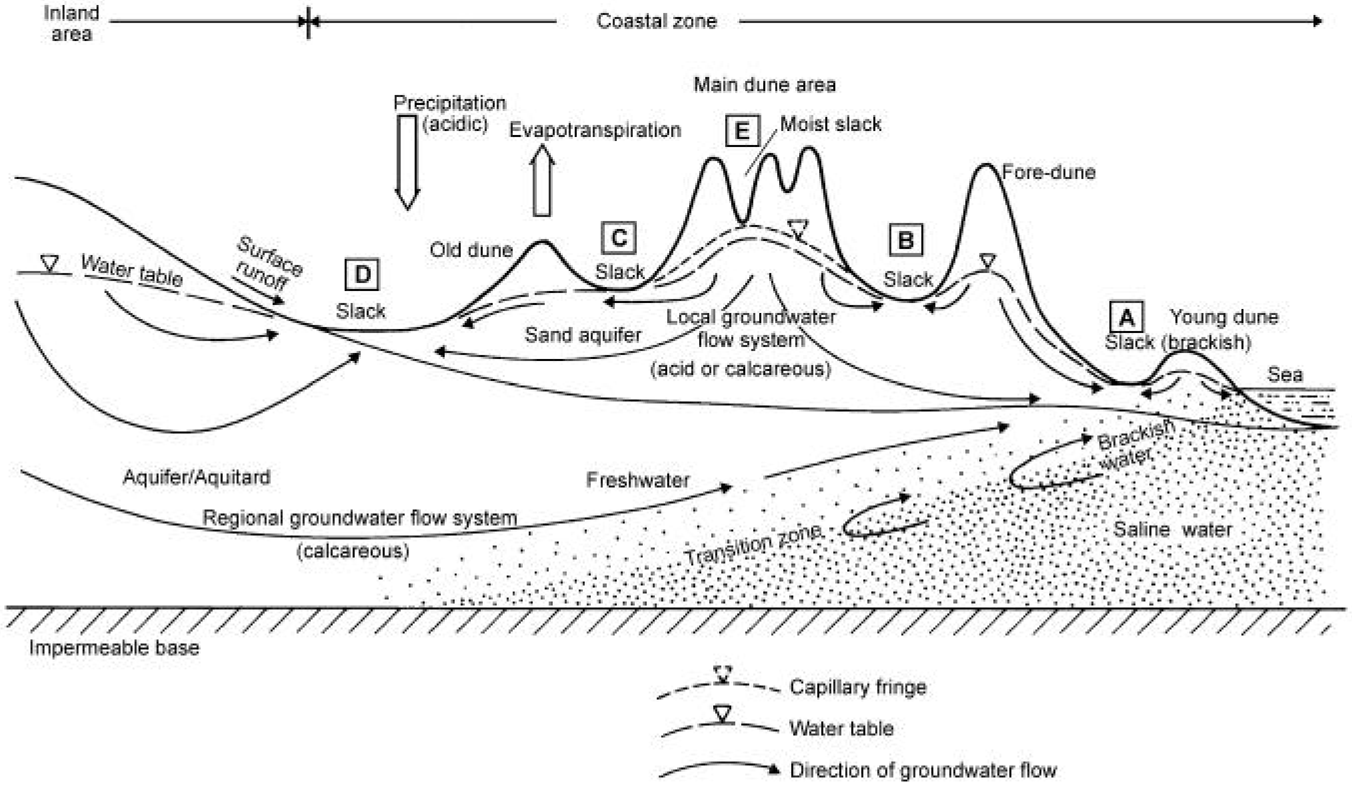

Figure 4.1 Conceptual model of hydrological and hydrogeological controls on humid dune-slack formation in coastal areas. See text for an explanation of dune-slack Types A, B, C, D and E.

Figure 4.2 An example of a Type B dune-slack at Winterton Dunes, Norfolk, in November 2005. (NB: colour versions of Figures 4.2 - 4.4 are available in the pdf version of this report).

Figure 4.3 An example of a Type D dune-slack at Horsey Dunes, Norfolk, in November 2005.

Figure 4.4 An example of a Type E moist dune-slack at Winterton Dunes, Norfolk, in September 2005.

Compared with the wetland framework for Eastern England (Wheeler and Shaw 2000; Wheeler and others 2004) and as presented in Table 4.1, dune systems are not specifically identified, although WETMEC Type 3 (Fluctuating Seepage Basin) has similar hydrogeological characteristics to dune-slack Type B in that a shallow basin (interpreted here as a slack) intersecting the water table is subject to considerable vertical fluctuation in water level from swamp (>1 m depth) conditions at high groundwater levels to subsurface (dry) conditions when water tables are low. The degree to which basins dry out partly depends on their depth relation to the water table with some deeper examples permanently wet, except in exceptional conditions. WETMEC Type 4a ('Solid' Direct Seepage Percolation Basin) has some similarity with dune slack Type D in which a topogenous hollow at the base of a seepage slope (interpreted here as the coastal margin of the inland area) receives a permanent seepage of groundwater. In order to distinguish between the dune-slack classification presented in this report and the wetland classification presented by Wheeler and Shaw (2000), it is recommended that the conceptual model presented in Figure 4.1 is adopted as the hydrological and hydrogeological classification of humid dune-slacks.

In comparison with examples described in the literature, the sketch sections shown in Figure 4.5, 4.6 and 4.7 are related to the generic types described above.

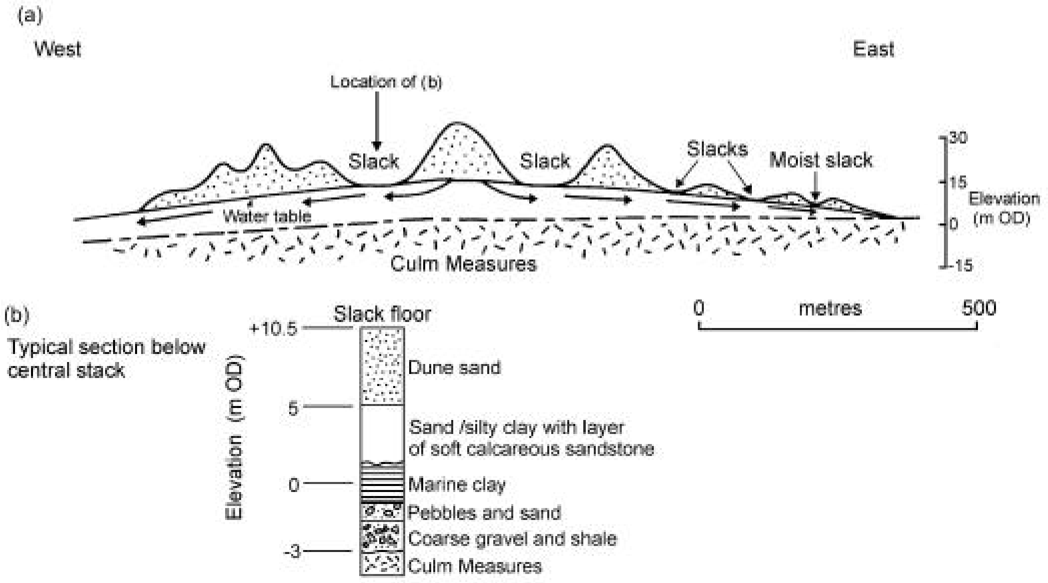

Figure 4.5 Dune features at Braunton Burrows, Devon: (a) lithological section through the central slack within the main dune area and (b) cross-section of the dune area showing the relationship of the dune-slacks to the water table together with inferred directions of groundwater flow. Based on May (2003).

Table 4.1. Comparison of classification of humid dune-slack types presented in this report and the WETMEC classification of wetland types (Wheeler and Shaw 2000; Wheeler and others 2004). Also shown is the sensitivity of dune-slack types to changes in hydrological conditions

Dune-slack type (this report)	Description	WETMEC wetland type	Description	Comparison between dune-slack type and WETMEC type	Sensitivity to hydrological change with respect to water table elevation/water balance fluxes
A	Seaward, young dune-slack potentially subject to brackish conditions	-	-	No comparison	Low sensitivity since likely to be of an ephemeral nature as young dune advances landward
B	Precipitation-fed slack situated in a dune hollow formed by a blow out or successive dune formation landwards. Groundwater flow directed to the slack with water then lost by evapotranspiration	3	Fluctuating seepage basin in a shallow topographic hollow that is subject to a high degree of vertical fluctuation in water level	Similar	High sensitivity since affected by water table fluctuations in response to seasonal wet and dry conditions and/or external influences such as groundwater abstraction and land drainage
C	Flow-through slack. As for B but groundwater flows into the up-gradient edge of the slack, flows through the slack and then infiltrates at the down-gradient edge. Perched water table conditions above clay or peat layers can promote horizontal flow between adjacent slacks	-	-	No comparison	High sensitivity since affected by water table fluctuations in response to seasonal wet and dry conditions and/or external influences such as groundwater abstraction and land drainage
D	Slack at the boundary between the dune system and inland area with water levels buffered by regional and local groundwater flow systems	4a	‘Solid’ direct seepage percolation basin situated in a topographic hollow at the base of a seepage slope and receiving a permanent seepage of water	Similar	Moderate sensitivity since slack water levels are maintained by steady regional groundwater flow even during dry weather. Surface runoff may also contribute to a wet slack condition
E	Moist dune-slack situated at a high elevation in the main dune area	-	-	No comparison	Very high sensitivity since only in reach of moisture in the capillary zone with only occasional flooding during wet years under a high water table condition

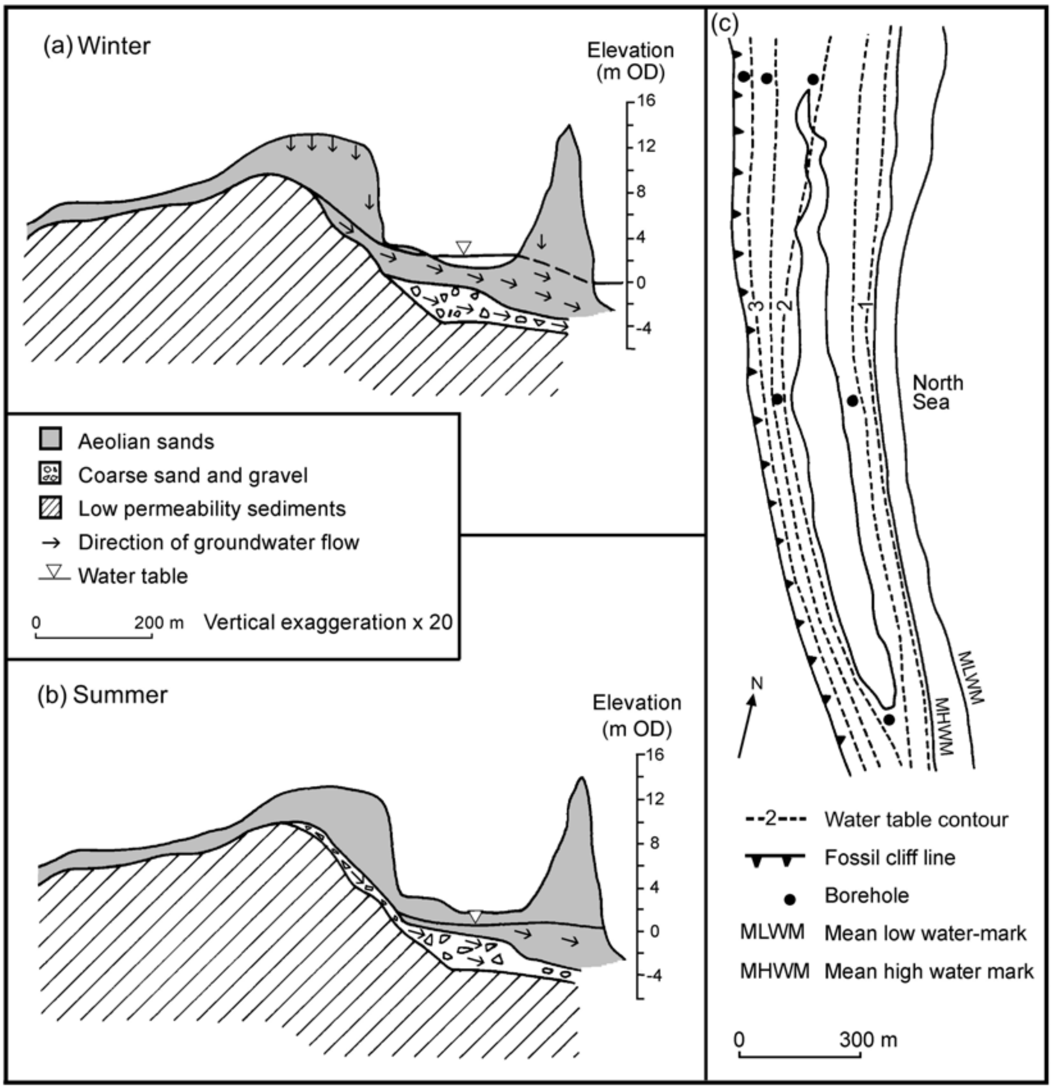

Figure 4.6 Conceptual model of (a) winter and (b) summer hydrogeological conditions at St. Fergus dunes and Winter Loch, Scotland, together with (c) map of water table contours for winter conditions showing a seaward hydraulic gradient (Soulsby and others 1997).

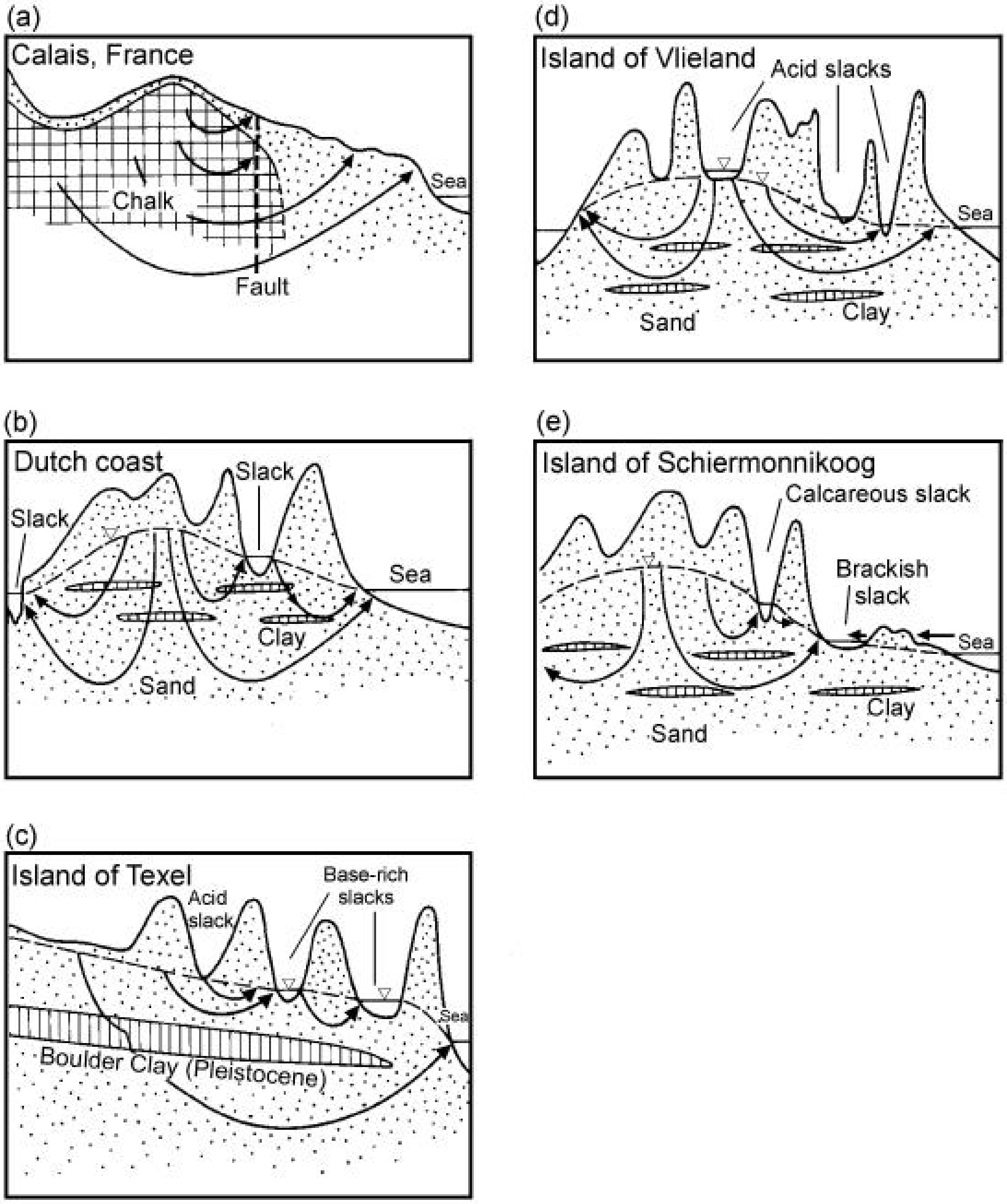

Figure 4.7 Conceptual models of hydrogeological conditions of coastal environments with dune-slacks. (a) Calais, France (after Bakker & Nienhuis 1990); (b) Dutch coast (after Stuyfzand 1993); (c) Island of Texel; (d) Island of Vlieland; (e) Island of Schiermonnikoog. Model sections (c), (d) and (e) are based on Grootjans and others (2001).

At Braunton Burrows, north Devon (Figure 4.5), and at the rear of the system, there is an extensive area of low dunes and slacks which may be extensively flooded in winter (Figure 4.5). The seaward dune ridge, usually rising to about 15 m OD is fronted by a line of fore-dunes rising to about 4.5 m OD. The elevation of the slacks is highest in the middle of the central zone of the dunes at about 9 m OD but falling in elevation northwards, southwards and seawards. The water table underlying the system is reported to be dome-shaped being some 6 m higher in the centre than at the margins. Willis and others (1959b) interpreted wind deflation as the cause of the lowering of the dune surface down to the elevation of the water table. The dunes at Braunton Burrows overlie both marine clay and gravels and sand resting on the Culm Measures bedrock. A preliminary interpretation of the hydrogeological conditions at Braunton Burrows would suggest that the dune-slacks are of Type C with groundwater flow radiating away from the domed water table ridge.

The annual pattern of groundwater flow in the St. Fergus dunes and Winter Loch in north-east Scotland is presented in Figure 4.6 based on Soulsby and others (1997). Maps of water table contours constructed from measurements of groundwater level at six water level recorders showed that winter flooding of the Winter Loch results from recharge of the unconfined aquifer in the aeolian sands. The groundwater recharge area is about 0.85 km^2 and includes the Loch itself, the western inner dunes and the eastern edge of a plateau and former cliffline. Vertical seepage during the autumn and winter is impeded by the impermeable glacio-lacustrine sediments underlying the dunes and the subsequent water table rise within the overlying sands that floods the low-lying Winter Loch. Given their north-south alignment, the St. Fergus dunes and Winter Loch act as an integrated groundwater system driven primarily by the west-east movement of groundwater from the former cliffline. The exfiltration of groundwater on the western side of the Loch and infiltrating water on the eastern side is typical of Type C dune-slack behaviour. In summer, the water table falls and the only groundwater discharge is as seepage along the beach face (Soulsby and others 1997).

Further examples of coastal aquifer systems containing dune-slacks are given in Figure 4.7 and represent a Chalk aquifer in France, a Dutch coastal area and the Wadden Sea islands. In the example from near Calais (Bakker and Nienhuis 1990), a supposed geological fault in the subsurface Chalk is present causing groundwater to discharge as springs (Type D slack). Sand dunes in front of this older landscape receive calcareous groundwater and this gives rise to the existence of several calcareous dune-slacks.

The model of Stuyfzand (1993) in the Dutch coastal area is just one example of many studies showing a through-flow slack (Type C) in a calcareous dune area. The model of the Island of Texel (Grootjans and others 2001) shows an old boulder clay layer, the remnants of glaciation, with part of the island representing an old Pleistocene landscape. A massive Holocene dune system has been added with time as a series of dune ridges formed from current and earlier sand beaches. The process of dune formation is on-going with a whole range of primary dune-slacks in existence, from brackish to fresh calcareous and acid groundwater-fed slacks.

The models of the Islands of Vlieland and Schiermonnikoog (Beukeboom 1976) show massive dunes that represent Holocene sand and clay layers. These islands migrate in a westerly direction due to erosion/accretion processes. Vlieland has very little carbonate material in the beach sand (0.05% $CaCO_3$) such that the dune sand is virtually leached of carbonate content. On Schiermonnikoog a very young dune-slack (<50 years) is present, which receives calcareous groundwater from the main dune body and is regularly flooded by brackish water or even sea water in the winter.

4.1.2 Dune-slack water balance model

Generally in wetland ecology, the lowest groundwater level, fluctuation in water levels and inundation periods are used to evaluate or predict vegetation composition and vegetation change and this is no different for dune slack communities (Jones 1993). In considering dune-slack vegetation, Lammerts and others (2001) argued that these variables are of limited value because they depend on yearly climatological differences and because species often respond to only one or two of these variables and thus cannot be easily compared. Lammerts and others (2001) proposed three alternative variables that are of use in understanding dune-slack hydrology (see Figure 4.8).

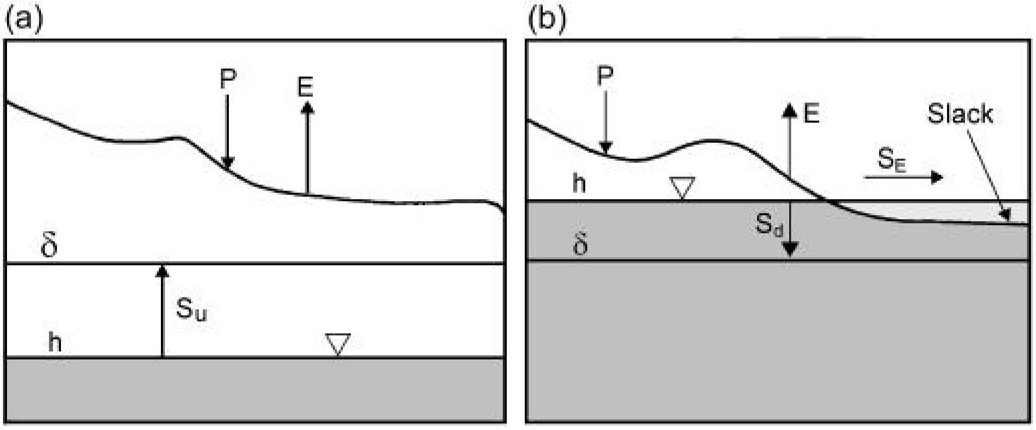

Figure 4.8 Dune-slack transects representing the relationship between site-specific water flows, S, the water table elevation, h, and the local hydrological base level, d, under the condition of a mean precipitation surplus $\left(\overline{P-E}\right)$. In (a) the groundwater level is low and water is gained from the surroundings. In (b) the groundwater level is high (exfiltrating in the lower part of the slack) and water is lost to the surroundings. S_u represents upward seepage ($S > 0$), S_d and S_s represent downward seepage and surface runoff ($S < 0$ in both cases). From Lammerts and others (2001).

These variables are: (i) local hydrological base level, d; (ii) seepage conductance, s; and (iii) yield factor, n. The first two variables describe, for mean climatological conditions at a site, how much water is gained or lost to the surroundings of the site due to upward or downward groundwater seepage. Recognising dynamic groundwater conditions, the seepage conductance represents the rate of seepage change with changing groundwater level. The gain or loss of water is thus given by: $S = (h - d)s$ where S is seepage flux (in cm/day), h is groundwater level (in cm with reference to the ground surface), d is local hydrological base level (in cm with reference to the ground surface), σ is seepage conductance (in cm/(day.cm)). The yield factor, n, is dimensionless, and determines the quantity of water released from storage when the water table falls and is calculated from the following water balance equation:

$$\Delta h = ((P - E + S)/n)\Delta t$$

where Dh is the change in groundwater level in time internal Dt, and P, E and S are the mean daily precipitation and evapotranspiration and mean daily seepage in the same time interval, respectively.

In many water balance studies, the accuracy of calculations is often dependent on the quality of hydrological data, for example the availability of coastal weather station and soil characteristics data, to enable calculation of actual evapotranspiration rates and soil water deficit values. In a pragmatic study using basic meteorological and hydrogeological data, Clarke & Pegg (1993) were able to estimate, using a simple water balance approach and Darcy's Law, the rate of groundwater flow from a section of the Ainsdale sand dunes. Conditions for a very dry summer and very wet winter were considered with outflow per unit width of a typical sand dune section varying between 0.68 m^3 day^{-1} (summer) and 0.82 m^3 day^{-1} (winter), equivalent to values of 127 mm a^{-1} and 158 mm a^{-1}, respectively, for the whole of the sand dune area. The study concluded that there is a delicate balance between the components of the groundwater system at Ainsdale that are very sensitive to the controlling climatic parameters: levels of standing water are almost entirely dependent upon the effective rainfall in the preceding months; and very rapid changes in state occur with transformation from dry to wet conditions possible in only a few days, as reported for September 1976 (Clarke and Pegg 1993).

4.1.3 Groundwater abstraction and other hydrological impacts

Variations in the extent and duration of flooding of the dune surface are important in determining vegetation species composition and structure and in maintaining suitable breeding conditions for aquatic species. Any disturbance of this regime will affect the eco-hydrological condition of humid dune-slacks.

The conceptual model of dune-slack types shown in Figure 4.1 demonstrates the significant reliance of dune-slacks on the maintenance of a high water table. The sensitivity of dune slacks to hydrological change is summarized in Table 4.1 with respect to variation in water table elevation and fluxes in the water balance. Temporally, and under variable climatic conditions, water levels in dune-slacks are expected to fluctuate in response to the balance of precipitation and evapotranspiration over the dune surface. This dependency is illustrated in Figure 4.9 with the depth of water in a dune-slack at Winterton, Norfolk, increasing in as little as two months in response to autumn groundwater recharge. The higher the position of the dune-slack within the main dune system then the more likely that it is to experience periods of drying-out, as exemplified by Type E. Under natural flow conditions, dune-slack Type D is likely to remain wet for the longest period in that it is partly supported by the larger regional groundwater flow system.

(a)

(b)

Figure 4.9 Comparison of water levels in a dune-slack at Winterton Dunes, Norfolk, on (a) 14 September 2005 and (b) 20 November 2005. The water level has risen by a few centimetres in the intervening two-month period in response to the onset of autumn recharge. The general hydrochemical condition is fresher with the absence in November of the ferruginous algal growth which was evident in September. (NB: colour versions of these photographs are available in the pdf version of this report).

Given the tendency towards an ephemeral nature, then any external influence on groundwater levels or recharge rates within or adjacent to a dune system is likely to adversely affect the existence of dune-slacks. Such external activities include groundwater abstraction for municipal, agricultural, industrial, military and recreational purposes and dewatering of groundwater for land drainage control and quarrying activities. In addition, and as reported for Newborough Warren, Anglesey, changing land use in sand dunes, for example planting forest, can alter rates of interception and evapotranspiration and therefore groundwater recharge. A groundwater model constructed for Newborough Warren showed that potentially removing forest in the topographically high area in the north of the reserve would allow greater recharge that would benefit groundwater levels across the Warren and so help maintain dune-slacks (Betson and others 2002; Bristow 2003).

According to Pye and Saye (2005), geomorphological changes to Welsh sand dunes under rising sea-level due to climate change may also impact the hydrogeology of dune systems. Two opposite effects are identified: (i) the lowering of fresh groundwater levels as a result of coastal erosion and narrowing of the dune belt leading to drier conditions and deflation of the dune surface; and (ii) rising sea-level causing an increase in groundwater levels. The balance of these two effects is dependent upon the characteristics of the dune area, the amount of erosion and the degree of sea-level rise (van der Meulen 1990). A rising water table in response to an increase in sea-level may be expected to favour humid dune-slack species and to encourage sand stabilisation in low-lying areas (Pye and Saye 2005) although saline water intrusion may cause brackish conditions in coastal slacks such as Type A (Figure 4.1).

A hypothetical, detrimental situation is shown conceptually in Figure 4.10 in which an abstraction borehole is situated at the coastal margin of the inland area. As a result of the decrease in the elevation of the water table under pumping conditions, dune-slacks of Types B and C have disappeared (compare with Figure 4.1). Only Types A, D and E (formerly Type B) are represented, with Type A potentially more seriously affected by brackish water due to increased saline intrusion induced by groundwater abstraction (Q). The volume and hydrochemical characteristics of dune-slack Type D is altered by the absence of a groundwater input and the fact that the inflow of surface runoff from the inland area is able to infiltrate the permeable base of the slack.

To illustrate with a case study, the history of groundwater abstraction along the Dutch Coast and its consequences for the remaining dune-slacks is presented in Appendix 2 based on the Wadden Sea islands of Schiermonnikoog. Here, eco-hydrological research has been carried out in the framework of a large project aimed at finding solutions for the conflict between drinking water supply and nature conservation.

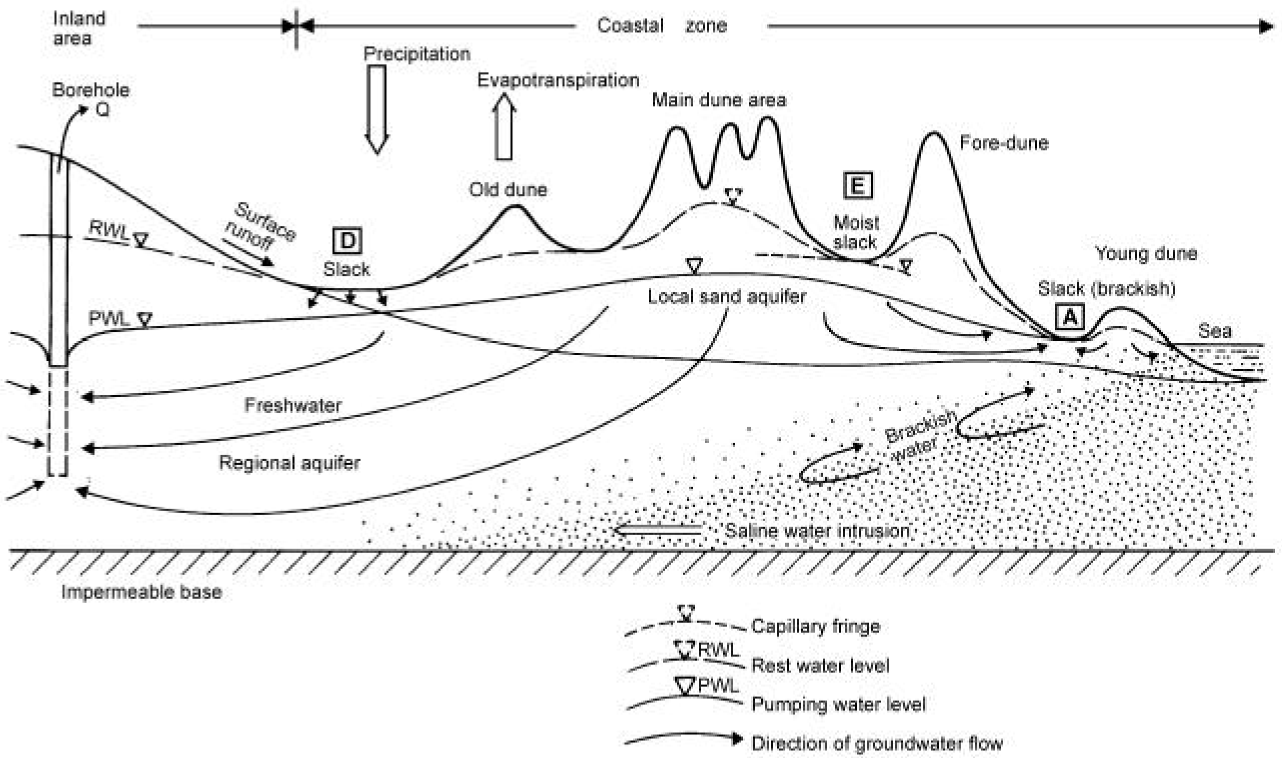

Figure 4.10 Conceptual model of the impact of groundwater abstraction on the hydrological and hydrogeological conditions of dune-slacks in a coastal area. See text for an explanation of dune-slack Types A, D and E and compare with Figure 4.1 which shows natural dune-slack conditions without pumping.

4.1.4 Hydrochemistry of dune-slacks

Research into the hydrochemical controls of dune systems is less well studied in the United Kingdom and so the following section is largely based on intensive research completed in the Wadden Sea islands. The hydrochemical composition of dune-slacks will be affected by salinity but will also be influenced by the alkalinity of the local and regional groundwater flow systems. The calcareous nature of regional groundwater flow derived from an inland area will create a base-rich slack. Also, dune-slacks will be either acidic or calcareous depending on the carbonate content of the dune sand. Dune sands containing shell material are expected to be calcareous. Factors that stabilise the longevity of pioneer stages of dune-slacks comprising many Red List species are usually associated with a regular supply of mineral-rich groundwater.

The influx of anoxic and iron-rich groundwater is important for vegetation succession. Lammerts and others (1995) showed that pioneer stages were much more stable in groundwater-fed dune-slacks compared to slacks that were situated in infiltration areas. They hypothesised that the discharge of groundwater in spring and early summer keeps the soil moist so that laminated microbial and algal mats do not dry out (van Gemerden 1993). It is known that algal mats can stabilise sandy substrates during the very early stages of dune-slack formation (Pluis and de Winder 1990). When growth leads to the formation of visible layers these are called microbial mats. Prerequisites for the growth of microbial mats are the availability of water, much light, and the absence of excessive erosion and consumption by animals. Optimal growth conditions occur on bare soils that are regularly flooded or attain sufficient moisture by capillary water supply. Cyanobacteria in microbial mats can fix nitrogen (Stal and others 1994) and the mats may develop in a relatively short period.

In an intensive study, Adema and others (2002) measured sulphide and oxygen concentrations in a dune-slack on the Wadden Sea Island of Texel in the Netherlands, using micro-electrodes (see Figs 4.11 and 4.12). They found that on the infiltration side of the slack where the topsoil had been decalcified, the sulphide concentrations reached toxic levels (30-90 µmol/l) for some higher plants, in particular sedges (Lammerts and others 1999). Plants that could grow at the infiltration side of the slack were common reed (*Phragmites australis)* and small pioneer species, such as *Samolus valerandi* and *Littorella uniflora*. At the exfiltration side, no sulphide was measured, although the redox potentials were much lower than in the infiltration site, due to continuous inflow of anaerobic and iron-rich groundwater. The authors argued that the iron-rich groundwater fixed the free sulphide produced by the microbial mats by forming iron sulphide. At the infiltration side, however, no iron was present and free sulphide could accumulate. These relatively high sulphide concentrations did not harm common reed, nor the pioneer species, since they are capable of oxidising sulphide to sulphate by releasing oxygen from their roots (radial oxygen release). The sulphide production in the infiltration areas can, however, release phosphates in the iron-depleted topsoil due to binding of sulphides with iron (Lammerts and others 1999). The infiltration side of such a slack, therefore, cannot maintain pioneer vegetation for a long time and tall reed vegetation will soon take over.

A stable pioneer vegetation existed for over 60 years on the Island of Texel between the exfiltration and central parts of dune-slacks because the pH is buffered, sulphide production is neutralised by iron, and acidification is prevented by discharge of calcareous groundwater. Sival and others (1998) found that at exfiltration sites of dune-slacks secondary, *in situ* carbonate deposition occurred in the early stages of dune-slack succession.

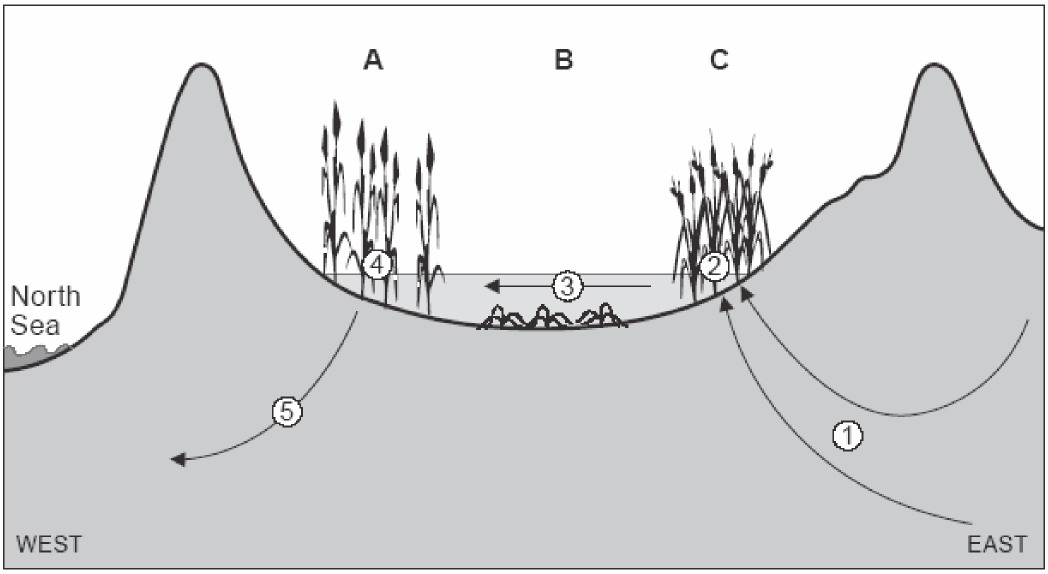

Figure 4.11 Schematic presentation of a flow-through dune-slack on a Dutch Wadden Sea island. In this particular case the vegetation zonation has been derived from the dune-slack 'De Buiten Muy' on the Island of Texel. **A** = stand of common reed *Phragmites australis*, **B** = pioneer stage with *Littorella uniflora*, **C** = tall sedges with *Carex riparia*. 1 incoming calcium- and iron-rich groundwater; 2 exfiltration of groundwater; 3 precipitation of iron and calcium; 4 infiltration of iron- and calcium-poor surface water; 5 sulphate reduction during infiltration (after Adema 2002).

The carbonate was deposited in a very thin layer on the mineral soil. Loss of carbon dioxide from the calcareous groundwater resulted in carbonate precipitation at the soil-air interface (Chafetz 1994), thus counteracting soil acidification in a very significant way. Such carbonate precipitation occurs when water tables remain and temperatures are also high. Under such conditions carbon dioxide escapes from the discharging calcareous groundwater or is taken up by algae, mosses or small water plants. Calcium carbonate is than deposited as a thin silty layer on the soil or even on the leaves of plants. As a result, and at the exfiltration side of the slack, the groundwater discharge contributes to maintaining a high pH, low nutrient availability, especially phosphate, and preventing toxic sulphide conditions.

Groundwater chemistry in a shallow coastal aquifer in north-east Scotland was monitored over the hydrological year October 1996-September 1997 as reported by Malcolm and Soulsby (2001). Hydrogeochemical analysis revealed that groundwater in the shallow sand aquifer was circum-neutral, and non-saline, despite being within 50 m of the sea and only 1 m above the mean high water mark. Calcium and bicarbonate were the dominant ions, reflecting weathering processes in the aquifer. Geochemical modelling indicated that calcite weathering of shell fragments within the sand was the primary source of calcium and alkalinity generation. The concentrations of sodium and chloride were also important, explained primarily by atmospheric inputs from precipitation.

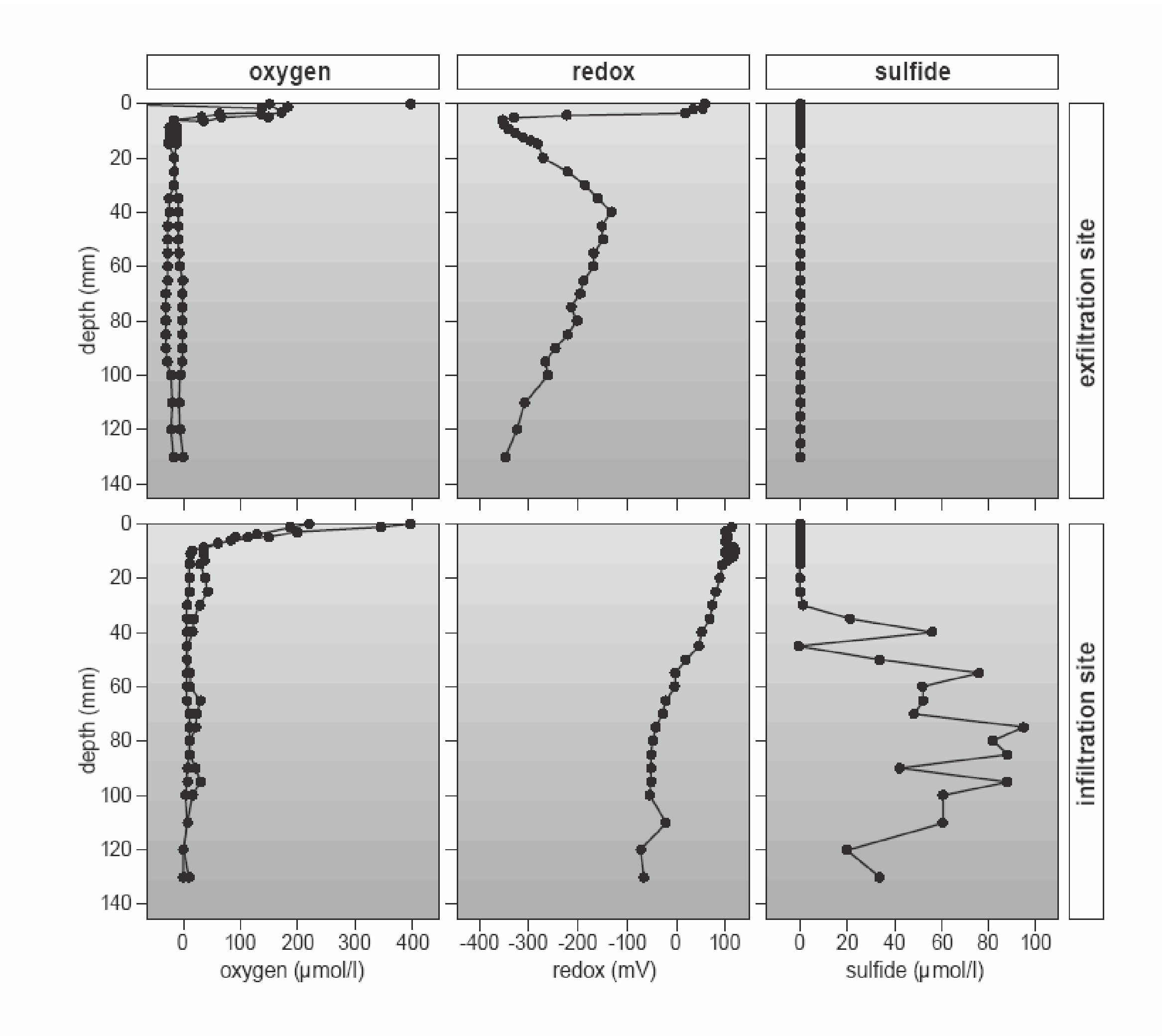

Figure 4.12 Oxygen content, redox-potential and sulphide concentrations measured in soil profiles in exfiltration and infiltration sites of dune-slack 'De Buiten Muy' on the Island of Texel in The Netherlands (after Adema 2002). No free sulphide was measured in the exfiltration despite lower redox potentials. Apparently the toxic sulphide is bound by a regular supply of iron in the discharging groundwater.

Malcolm and Soulsby (2001) commented that the spatial and temporal variation in groundwater chemistry was remarkably complex for what intuitively appeared a simple aquifer system. Temporal variations in groundwater chemistry mainly related to the seasonal event of groundwater recharge. Thus, the main period of rising groundwater levels in the autumn and winter resulted in a marked dilution of solutes in the aquifer, implying that water storage greatly increased in a relatively short period. A period of several weeks appeared to be required for dissolution processes to proceed to equilibrium. Spatial variation in groundwater chemistry appeared to relate to the spatial distribution of geochemical processes in different hydrogeological units. Sulphate reduction, alkalinity generation and iron precipitation appeared to be locally important processes. Malcolm and

Soulsby (2001) also concluded that increasing pressures in the coastal zone dictate that pollution can threaten the integrity of hydrochemical processes of coastal aquifer systems and requires careful monitoring if freshwater wetlands are to maintain their conservation importance.

4.2 Comparison of British dune slacks with those of the Wadden Islands

4.2.1 Rationale

Although there is a substantial body of modern work on the eco-hydrology of European dune slacks, little of it has been carried out in Britain, where with some notable exceptions dune slacks have been neglected scientifically. In contrast, much eco-hydrological research has centred on dune systems on the islands of the Wadden sea, along the North-Sea coasts of Denmark, Germany and the Netherlands. The relative lack of local information raises important questions as to the relevance of such work for the setting of ecological targets for British habitats. Where direct comparison is not possible, tests of comparability might potentially be framed in four ways.

- Geomorphological and physiographic setting, as an indication of potential water supply mechanisms
- Composition of substrate, as an indication of buffering capacity and water retention
- Composition of the plant communities and the extent to which they represent the Habitat Directive Annex I feature types
- Presence of rare and threatened species listed in Annexes II and IV of the Habitat Directive.

4.2.2 Geomorphological and physiographic setting

Slacks are integral components of the dune systems in which they are found and therefore the geomorphological setting of a system is bound to influence the hydrological characteristics and mechanisms of its slacks. Most British dune systems, like their other NW European counterparts, have formed in the last 6-7000 y, where substantial seabed deposits could move on to the beach (May 2003). They have formed on platforms of marine clay, peat, shingle, or harder rock.

A range of physiographic types can be recognized in Britain (Ranwell 1972; May 2003). Foreshore dunes are essentially prograding and project seawards from the shore on offshore islands, spits and nesses. New dune ridges tend to form to seaward and eventually become stabilized *in situ*. Hence a new slack can form behind each seaward ridge and tends to remain in the same position. Hindshore dunes develop in bays and on exposed sandy coasts, where there are abundant sand supplies and strong onshore winds. New dunes grow to a height where they eventually experience more erosion than deposition and begin to migrate landwards and lose height. Stabilization occurs when a dune is sufficiently deflated to form a low plain, inland. Slacks form on a cyclic basis as the level is eroded down to damp sand between ridges. Erosive blowouts can cause a ridge to fragment into a series of parabolic dunes, with low-lying slacks between parabolas. On the Wadden Sea islands the situation is fundamentally similar, except that the processes are more dynamic, since the whole islands (with their dune systems) can move under the influence of erosion on the west side and accretion on the east side. In Britain dunes have generally developed on a less mobile coastline. Size of the dune system is also important and so it is probably reasonable to extrapolate from the Wadden Islands only to the larger British systems.

4.2.3 Composition of sediment

Although coastal dunes are typically thought of as composed of silica sand, as explained previously, the calcium carbonate content is extremely important. Calcium carbonate is extremely variable between and, to an extent, within systems (May 2003). It can derive from the erosion of calcareous rocks but in many places is due to the incorporation of shelly debris brought ashore by waves and onshore winds. Foredune sands usually have the highest amounts, as carbonates are progressively dissolved and leached away in older dunes. Foredune sands on the coast of England and Wales are generally low in calcium carbonate but most on the west coast have at least 1% and values of 10-20% are common; on the exposed south-west coast, calcium carbonate can comprise 50% of foredune sand and even higher contents characterize the machair of Scotland (May 2003). Dunes of the East coast of England, with prevailing offshore winds, tend to have the lowest calcium carbonate contents. However 0.3% represents sufficiently buffering to produce calcareous systems and most British dunes share this feature with their Wadden Island counterparts.

4.2.4 Community structure

A comparison of British (Rodwell 2000) and NW-European (Petersen 2000) dune slack communities suggests that some British types are quite similar to the Dutch, German and Danish types, but that others are rather different (Appendix 1). Rodwell's classification provides only two clear successional stages: SD13 (calcareous pioneer) and SD 14-17 (more mature stages) but no late successional types.

SD13 is well characterized, by *Sagina nodosa, Centaurum erythraea, Aneura pinguis* and *Bryum pseudotriquetrum*. It differs from the Dutch and German pioneer stages (which have *Centaurium littorale* and *C. pulchellum* and *Odontites vernus* as characteristic species. These pioneer communities often have brackish species, which point to there being an open connection to the sea. SD13 apparently does not have such brackish influences and appears to be isolated from the sea. So flooding and sand blowing must sustain this type.

SD14 is with respect to *Liparis loesellii* and other Red List-species the most important dune slack type. It has much in common with the Dutch and German *Caricion davallianae* communities in particular. SD14c is a successional stage following SD13 and it is most species rich. It lacks *Schoenus nigricans*, and *Juncus articus/balticus* though. In Wales, at least, the *Junco baltici-Schoenetum nigricantis,* with an aspect of *Schoenus nigricans* probably does occur, according to Rodwell. The Dutch and Gertman types differ in having species such as *Juncus alpino-articulatus, Juncus articus/balticus, Carex trinervis* and *Calamagrostis epigejos.* The English/Welsh types have a higher frequency of *Campylium stellatum, Equisetum variegatum, Epipactis palustris and Anagallis tenella,* but *Parnassia palustris and Dacthylorhiza incarnata* are less frequent. Both SD14 and the Dutch/German types show a faint influence of brackish species, indicating some connection to the sea. With respect to groundwater relations, both types are probably comparable.

SD16 is much more common in England; it also has many Red-List species and, belongs to an impoverished, much drier, form of the *Caricion davallianae* alliance. *Liparis loeselli* does not occur in this type (too dry). It has no brackish species, so apparently no influence from the sea. There is almost no flooding by rain or groundwater and the water tables drop deep during summer, so probably no groundwater supply in summer. SD16c is the best developed unit and has much in common with the European *Pyrola-Salicetum,* which can follow the *Junco baltici-Schoenetum nigricantis* successionally. It may be that SD16 is situated in relatively small dune systems, whereas SD 13/14 are situated in much larger dune areas with large hydrological systems.

SD15 is quite common in Britain. It is distinctly wet, usually flooded for more than 4 months, but lacks most *Caricion davallianae* species. Only *Epipactis palustris* and *Equisetum variegatum* are frequent in SD15b and SD15c. The occurrence of *Equisetum palustre* in SD15a and SD15d is remarkable and probably points to discharge of anaerobic groundwater. SD15 and SD17 have much in common. They are also relatively widespread in England and Wales (except SD17). These dune slacks are regularly and intensely flooded in winter and spring. SD 17 is found more to the north (more precipitation) and has much in common with the Dutch/Danish and German wet dune slacks. SD17 has much less *Salix repens* and more *Potentilla anserina*. Groundwater regime is possibly comparable to the Dutch/German type, but the substrate is generally more calcareous (Scottish machairs). SD17 appears to have often an open connection to the sea, which the Dutch, German and Danish *Caricetum trinervi-nigrae* slacks do not have. The sub type with *Caltha palustris,* is probably a transition to more eutrophic wet meadows, influenced by calcareous groundwater. Rodwell suggests affinity with the Elymo-Rumicion.

In the Rodwell classification several continental European dune slack types are missing or covered under different vegetation types. Conspicuously missing are the *Junco baltici-Schoenetum nigricantis,* which occur regularly along the German, Dutch, and Belgium coast. Rodwell states that such community does occur in Wales. Unpublished relevees of dune slacks show that *Schoenus nigricans* may occur in practically all dune slack communities of Rodwell, although in very low frequencies (P. Rhind, personal communication). The *Pyrolo-Salicetum* (an older stage, which is rather acid, but still with many typical dune slack plants) may also be present in northern areas in England.
Dune slack types of with an acid environment are lacking in the Rodwell classification; no information is available on the occurrence of acid pioneer stages (*Sphagno-Rhynchosporetum albae*) and older heathland stages (*Empetro-Ericetum*) in English dune slacks. Dune pond vegetation is also not represented in the British dune slack typology (possibly due to the NVC sampling selection methodology: see comments in European Commission, 2003). Dune slack ponds, whose levels do fall dry in dry summers, are present on almost all Wadden Sea islands. The most common supports the *Samolo-Littorelletum,* which occurs on most islands, although rarely along the main coast. Rare communities include *Echinodoro-Potamogeton graminei, Cicendietum filiformis* and various other types within the Littorellion. They occur within coastal heathlands on the Dutch and Danish islands.

Overall, there is general comparability between the dune-slack plant communities in Britain and the rest of NW Europe, particularly among the more calcareous ones that are of most conservation interest. However, there are also some very significant differences in vegetation types: most importantly, the acid types on the Wadden Sea islands appear to be lacking in England and Wales and these are not classified elsewhere as mires or heaths.

Also, the saline influence evident in the species composition of many Wadden communities is not well represented in the British descriptions.

There are undoubtedly some underlying differences, perhaps associated with differences in physiographic setting, management and history, but these are confounded with lack of information on systems in England and Wales. The NVC type SD13 was defined on the basis a total of 48 samples (relevees); the species-rich SD14 had 246 samples, SD15 229, SD16 203 and SD16 142 samples (Rodwell 2000). A recent examination of the rare *Juncus balticus* at its only English station in the dune slacks of the Sefton Coast has underlined the limitations of the current NVC classification (Smith 2006b). The fit of 35 samples to NVC types (including SD13, 14, 15, 16 and 17) was generally poor or very poor, with only one being very good (81% fit for SD15) and two good (75 and 78% fits for SD15).

4.2.5 Rare and endangered species

The Natterjack toad (*Bufo calamita*) is a flagship species of British dune slack habitats. It is listed in Annex IV of the Habitats Directive. Archaeological remains indicate that it was once widespread in the Wadden Sea area. Despite large changes to the landscape made in the late Middle Ages (diking and damming) it apparently persists there but it is specifically restricted to some dune districts on the islands (Prummel and Heinrich 2005). This is clearly a close parallel with the British situation.

The fen orchid (*Liparis loeslii* – Annex II: 1903) is characteristic of base-rich, early to middle successional dunes at sites in both Britain and the Wadden Islands. Its behaviour and ecological distribution are extremely similar. The liverwort, petalwort (*Petalophyllun ralfsii* - Annex II: 1395) is very rare in early successional situations in Britain (see 3.9) but has not reported from the Wadden Sea. However, there seems to be remarkably little information on this species for anywhere in Europe.

4.3 Evaluation of restoration projects on the Dutch coast

The conventional paradigm of conservation is aimed at preventing or minimizing losses of habitat, species or system functioning. Anything short of (unrealistic) complete success will lead at best to gradual attrition of natural systems and species, unless there is also a capacity for ecological restoration (Perrow and Davy 2002a; b). Consequently, an evaluation of our capacity to restore systems should be part of any assessment. The complex interplay of hydrology, hydrochemistry and successional development previously outlined suggests that restoration is likely to be successful only within a narrow range of circumstances and this has been amply confirmed by experience on the Dutch coast. A conceptual model for the occurrence of endangered species in projects of varying success is shown in Figure 4.13.

(1) Unsuccessful projects include restoration projects where measures have been carried out at unsuitable sites; the seed banks were depleted and dispersal mechanisms were not effective in re-colonization. Most of these projects were carried out to compensate for losses in existing nature reserves.

(2) Temporary success, followed by rapid decrease of typical dune slack species can be observed in areas where seed banks were still present and dispersal mechanisms were effective, but where soil conditions and hydrological regimes were sub-optimal. Examples

are fresh water slacks surrounded by decalcified dune areas, where many changes in the hydrological regime had occurred.

(3) Successful reconstruction of dune slacks has mainly occurred in areas with hydrological systems that had been little influenced by man and where dispersal mechanisms were effective. Pioneer stages, however, were relatively short-lived.

(4) Very successful projects are where many typical dune slack species have established in large numbers and persisted for many decades. Examples include the large sandy beaches on the Wadden Sea islands that were enclosed by artificial dikes of drift sand. Local and regional species pools were available and dispersal mechanisms were still effective. There are also such successful projects in the calcareous dune areas of the mainland coast.

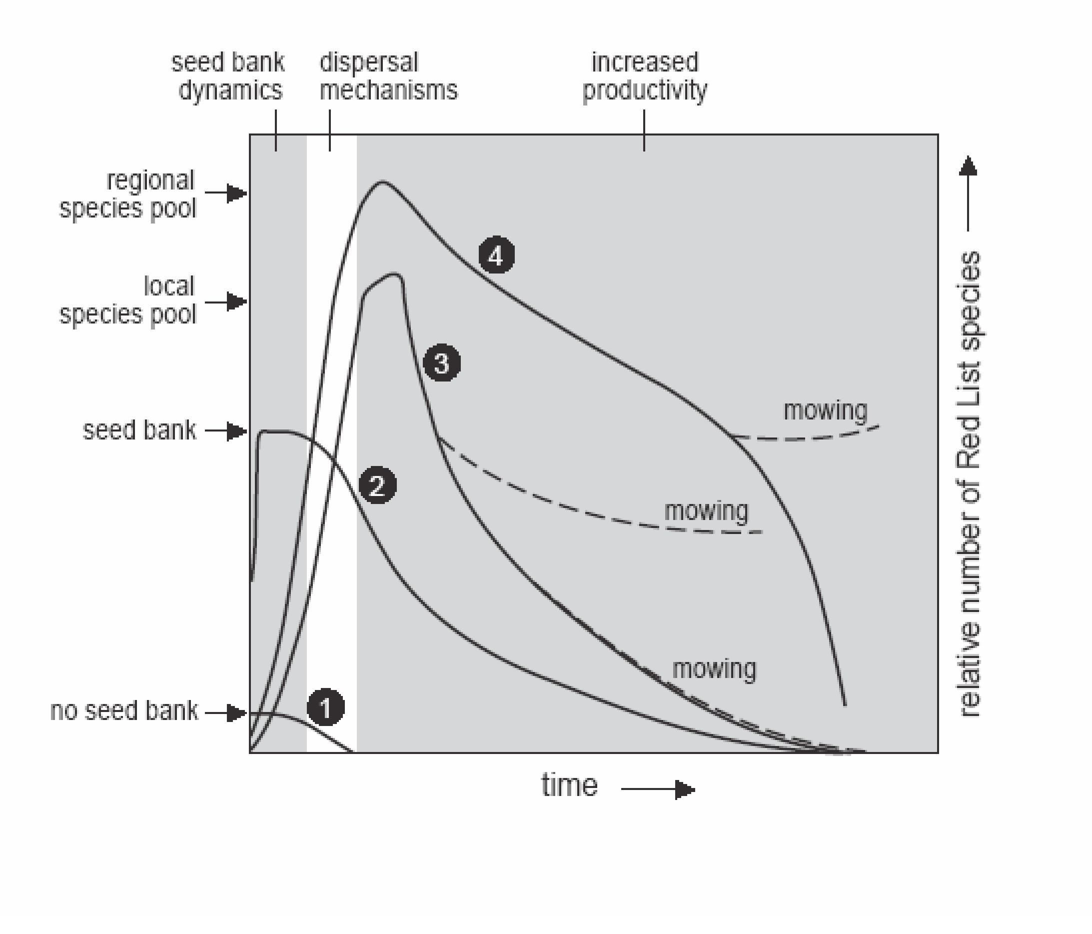

Figure 4.13 Conceptual model of occurrence of endangered dune slack species (Red List species) after restoration measures have been carried out. 1 = unsuccessful projects where measures have been carried out in unsuitable sites and where seed banks are depleted. 2= temporary success, followed by rapid decrease of target species is encountered in slacks where environmental conditions are unfavourable, but where seed banks were still present. 3 = successful, but short-lived, reconstruction of pioneer vegetation with many Red List species. Dispersal mechanisms are effective, but environmental conditions are sub-optimal. Mowing may sometimes retard a rapid spread of later successional species and a rapid decline in Red List species. 4 = very successful projects where many typical dune slack species establish in large numbers and persist for many decades. Natural processes retard

the succession towards late successional stages. A mowing regime may stabilise the pioneer stage even longer (Grootjans and others 2002).

When the availability of nutrients in newly created slacks is high during the first successional stages, or when natural slacks have been polluted, fast growing plants species, such as *Phragmites australis*, *Calamagrostis epigejos*, or even *Urtica dioica* (van Dijk and Grootjans 1993) can establish almost immediately and effectively store nutrients in living and dead material. The period for establishment of slow-growing pioneer species is often so short that conditions for them have become unfavourable even before most of the species have reached the area.

5 Research requirements

This review has highlighted the remarkable lack of research on British, as opposed to NW European, humid dune slacks. This is the case notwithstanding the considerable, sustained effort that has been put into understanding dune systems generally and other type of freshwater wetlands. In order to advance understanding of the hydrological and hydrogeological controls on the existence of these dune-slacks, further review work is necessary to confirm the conceptual model developed for dune-slack types and presented in Figure 4.1. This work should include a desk study and field visits to catalogue and classify the dune-slacks present in British dune systems. Long-term hydrological records for Ainsdale NNR, Braunton Burrows and Newborough Warren NNR might be included in this study.

Following from the above recommendation, and given the lack of systematic collection of hydrometeorological and hydrogeological data for British dune-slacks, a number of field sites should be established to collect hydrogeological information to examine the relationships between water levels and habitat functioning. These field studies should also establish a water balance for dune-slack types and derive recommendations for habitat protection based on measures of water level, frequency and severity of flooding and drought, and the magnitude of water flux in dune-slacks.

In association with detailed hydrological studies, both spatial and subsurface hydrochemical sampling of dune-slack systems is required to establish the pH and redox conditions that affect the alkalinity and concentrations of redox-sensitive species that influence dune-slack habitats.

A critical review is needed of dune slack types in Britain, such that vegetational types can be placed in successional sequences that are related to site calcareousness (pH) and wetness. A model for such a framework has been provided for the Wadden Islands and this is summarized in Figure 5.1 (Petersen 2000). A reappraisal of dune slack vegetation types could usefully begin with a desk study, as there is clearly a body of primary data in unpublished reports and theses. It would also need a programme of field studies involving the collection of new NVC compliant data from under-represented areas and communities (especially acidic areas and those influenced by saline water).

The habitat requirements and ecological responses of certain of the Annex 2 species are very poorly understood. In particular, an autecological study of *Petalophyllum ralfsii* could underpin efforts to ensure its survival in Britain. Another priority should be further studies on the ecohydrological requirements on *Liparis loeselii* var. *ovata*. Similar studies on British populations of other characteristic and rare species of dune slacks are highly desirable (eg *Equisetum variegatum*, *Pyrola rotundifolia*, *Moerkia hibernica*, *Dactylorhiza praetermissa* and *D. purpurella*).

Another key gap in scientific understanding could be filled by experimental studies into the practicalities of restoring or reconstructing the communities and eco-hydrological functioning of dune slacks within dune ecosystems. Apart from its intrinsic utility, restoration also represents the most rigorous test of progress towards scientific understanding.

Perhaps the strongest message to emerge from this review is the urgent need for integration of the science. Ecological studies need be closely associated with the hydrological and hydrochemical investigations suggested previously in order to gain a good understanding of how British dune slacks work, and the limitations on their communities and on particular plant and animal species.

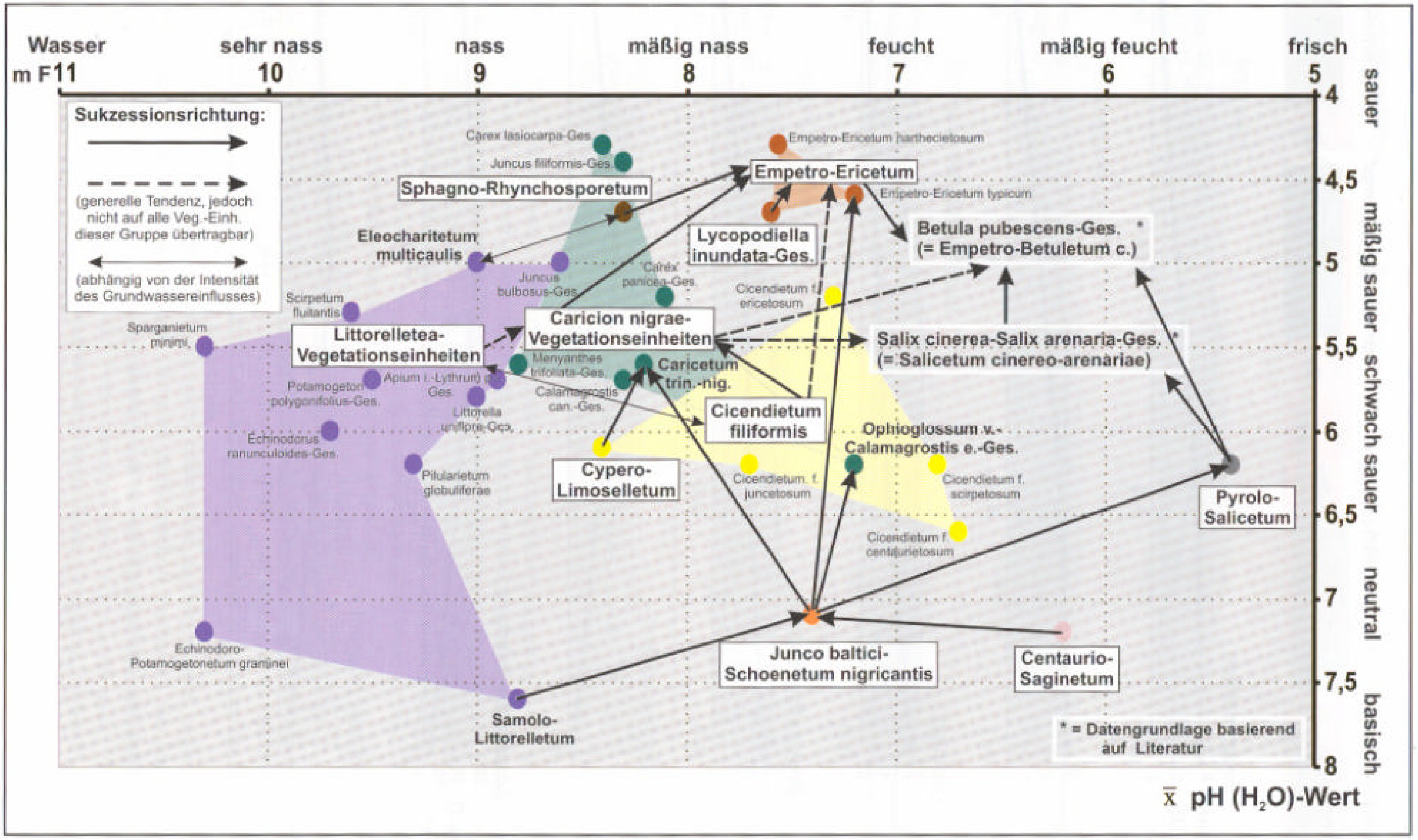

Figure 5.1 Characterization of NW European (Wadden Island) community types according to their wetness (horizontal axis) and pH (vertical axis). Successional relationships are shown by thick arrows (Petersen 2000) (NB: a colour version of this diagram is in the pdf version of this report.)

6 Interim ecological targets

The preceding review and critical evaluation have drawn attention, on the one hand, to the complexity of the eco-hydrology of European humid dune slacks and, on the other hand, to the paucity of information on British dune slacks. Consequently, it is not possible at this stage to set definitive ecological targets for the maintenance of site integrity and favourable species status for the habitats represented by NVC communities SD13-SD17. There are preliminary indications of the seasonal variations in water levels that differentiate these communities hydrologically (Table 6.1). Until such estimates can be refined and validated at a wider range of sites, where the hydrological mechanisms are understood, they represent approximate working targets for water level; however, they should not be interpreted as exact quantitative definitions.

Table 6.1 Summary of preliminary evidence on variation in water table depth in British dune slack communities (see section 3.2 for details and references)

NVC	NVC Name	Approximate winter water table depth (cm)*	Approximate summer water table depth (cm)
SD13	*Sagina nodosa-Bryum pseudotriquetrum* community	+2	-60 to -160
SD14	*Salix repens-Campylium stellatum* community	+10 to +50	-10 to -60
SD15	*Salix repens-Calliergon cuspidatum* community	+5	-40
SD16	*Salix repens-Holcus lanatus* community	0	-50 to -200
SD17	*Potentilla anserina-Carex nigra* community	+50	?

* Positive values indicate water tables above the soil surface ie flooding.

Practically useful eco-hydrolological targets may need to be expressed in terms of the frequency, magnitude and duration of deviation from the normal range (see section 3. 2) of the water table. Frequency is probably a key issue, because significant lowering over one annual cycle is likely to entrain irreversible changes. Magnitude and duration of outside the normal range needs to be assessed. Current indications suggest that lowering of the water table is not desirable for any dune slack communities. The precautionary principle suggests, as an interim target, that consents leading to lowering of the water table within dune slacks should be kept to a minimum (cf. the case history described in Appendix 2).

Hydrochemical targets are similarly uncertain. SD13 and SD14 depend on calcium-carbonate rich sands or calcareous groundwaters, and a pH of c. 7 or higher could be expected. SD15, its drier counterpart SD16, and SD17 appear to be typically less base-rich. The putative successional series and especially the demonstrably earlier stages (SD13 and 14) require nutrient-poor conditions; significant enrichment of groundwaters with nitrogen and phosphorus will engender or accelerate successional development to less desirable communities. Jones and others (2004) suggest a critical load for atmospheric N deposition on British dunes systems of 10-12 kg ha^{-1} yr^{-1}.

Although the range of British types may be less completely represented and they are certainly less well understood, it is now highly likely that they function in largely the same ways as European ones and are subject to the same sensitivities. The detailed conceptual framework developed here (section 4.1), although requiring practical confirmation, should usefully inform both the Habitats Regulations Review of Consents process and Common Standards Monitoring for site condition assessment. The five types of hydrological mechanism A-E have been defined on hydrological principles and still need to be related to UK vegetational communities; successional change can occur within each of these types.

Targets should take into account that:

- Dune slacks are part of a larger, dynamic eco-hydrological system, with a hydrological catchment, sand-dune mobility and a mosaic of successional change.
- The slacks that have most conservation interest (in terms of diversity and presence of specialised species) tend to be relatively early successional stages that depend upon periodic disturbance for renewal. Appropriate disturbance is likely only in large, active dune systems that have not been stabilized artificially; alternatively, management may be required to conserve them, provided that unacceptable successional change has not already rendered this ineffective.
- Nutrient enrichment derived from atmospheric deposition that becomes concentrated in infiltrating waters will accelerate successional development, as will that from polluted, eutrophic groundwaters.
- These sensitive slack environments depend on an interplay between infiltrating water and anoxic, calcareous groundwater. Lowering of groundwater can cause decalcification that has hydrochemical consequences that are as damaging as a lower water table alone would be.
- The areas of dune slack vegetation in England and Wales are very small (section 3.2): even small areas of loss or degradation will have a significant effect on site integrity.
- By far the most experience of the consequences of drinking water abstraction from coastal dune systems derives from The Netherlands. As is explained in a detailed case study (Appendix 2), the critical communities that include rare species such as *Liparis loeselii* have virtually no tolerance of a decrease in groundwater.

7 References and bibliography

ADEMA, E.B., ELZINGA, J.A. & GROOTJANS, A.P. 2004. Effects of microbial mats on germination and seedling survival of typical dune slack species in the Netherlands. *Plant Ecology*. 174, 89-96.

ADEMA, E.B. & GROOTJANS, A.P. 2003. Possible positive-feedback mechanisms: plants change abiotic soil parameters in wet calcareous dune slacks. *Plant Ecology,* 167, 141-149.

ADEMA, E.B., and others. 2002. Alternative stable states in a wet calcareous dune slack in The Netherlands. *Journal of Vegetation Science,* 13, 107-114.

ADEMA, E.B., and others. 2005. Enhanced nitrogen loss may explain alternative stable states in dune slack succession. *Oikos*, 109, 374-386.

ADEMA, E.B., VAN GEMERDEN, H. & GROOTJANS, A.P. 2003. Is succession in wet calcareous dune slacks affected by free sulfide? *Journal of Vegetation Science,* 14, 153-162.

AGNEW, A.D.Q. & GITAY, H. 1990. Resource pattern and community pattern in a dune slack grassland. *Spatial Processes in Plant Communities,* 191-199. The Hague: SPB Academic Publishers.

ARMSTRONG, W. 1975. Waterlogged soils. *In:* ETHERINGTON, J.R. ed. *Environment and Plant Growth*, 181-218. London: John Wiley & Sons.

ATKINS & ENTEC. 2003. *Water resources and conservation: A framework for the assessment of the hydrological requirements of habitats and species*. Environment Agency, English Nature & Countryside Council for Wales.

BAKKER, T.W.M. 1990. Geohydrology of coastal dunes. *In:* BAKKER, T.W.M., JUNGERIUS, P.D. & KLIJN, J.A. eds. *Dunes of the European Coasts*, 109-119. Cremlingen-Destedt: CATENA-Verlag.

BAKKER, T.W.M. & NIENHUIS, P.R. 1990. Geohydrology of Les Dunes de Mont Saint Frieux, Boulonnais, France. *In:* BAKKER, T.W.M., JUNGERIUS, P.D. & KLIJN, J.A. eds. *Dunes of the European Coasts*, 133-143. Cremlingen-Destedt: CATENA-Verlag.

BAKKER, T.W.M. & STUYFZAND, P.J. 1993. Nature conservation and the extraction of drinking water in coastal dunes. *In:* VOS, C.C. & OPDAM, P. eds. *Landcape Ecology of a Stressed Environment*, 224-260. London: Chapman & Hall.

BANKS, B., BEEBEE, T.J.C. & COOKE, A.S. 1994. Conservation of the natterjack toad *Bufo calamita* in Britain over the period 1970-1990 in relation to site protection and other factors. *Biological Conservation*, 67, 111-118.

BARDSLEY, L. & BEEBEE, T.J.C. 2001. Strength and mechanisms of competition between common and endangered anurans. *Ecological Applications*, 11, 453-463.

BARSOUM, N., and others. 2005. Eco-hydrological guidelines for wet woodland - Phase I. *English Nature Research Reports,* No 619. Peterborough: English Nature.

BEEBEE, T.J.C., DENTON, J.S. & BUCKLEY, J. 1996. Factors affecting population densities of adult natterjack toads *Bufo calamita* in Britain. *Journal of Applied Ecology,* 33, 263-268.

BEINKER, O. 1996. Zür Vegetationskunde der Dünen im Listland der Insel Sylt. *Kieler Notizen zur Pflanzenkundein Schleswig-Hostein und Hamburg*, 25/26, 128-166.

BEKKER, R.M., and others. 1998. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology,* 12, 834-842.

BEKKER, R.M., LAMMERTS, E.J., SCHUTTER, A. & GROOTJANS, A.P. 1999. Vegetation development in dune slacks: the role of persistent seed banks. *Journal of Vegetation Science,* 10, 745-754.

BERENDSE, F., LAMMERTS, E.J. & OLFF, H. 1998. Soil organic matter accumulation and its implication for nitrogen mineralization and plant species composition during succession in coastal dune slacks. *Plant Ecology,* 137, 71-78.

BETSON, M., CONNELL, L. & BRISTOW, C. 2002. *Groundwater modelling of Newborough Warren. The impact of forestry on coastal geomorphology at Newborough Warren/Ynys Llanddwyn NNR, SSSI, pSAC. Final Report for Countryside Council of Wales, Volume 5, Hydrogeology*. London: University College London and Birkbeck College.

BEUKEBOOM, T.J. 1976. *The hydrology of the Frisian Islands*. Free University of Amsterdam: PhD thesis.

BOORMAN, L.A. 1989. The grazing of British sand dune vegetation. *Proceedings of the Royal Society of Edinburgh,* 96B, 75-88.

BOORMAN, L.A. 1993. Dry coastal ecoststems of Britain: Dunes and shingle beaches. *In:* VAN DER MAAREL, E. eds. *Ecosystems of the World: Part 2A, Dry Coastal Ecosystems. Polar regions and Europe,* 197-228. Amsterdam, The Netherlands: Elsevier.

BOORMAN, L.A., LONDO, G. & VAN DER MAAREL, E. 1997. Communities of dune slacks. *In:* VAN DER MAAREL, E. eds. *Ecosystems of the World: Part 2C, Dry Coastal Ecosystems*, 275-293. Amsterdam, The Netherlands: Elsevier.

BOSSUYT, B. & HERMY, M. 2004. Seed bank assembly follows vegetation succession in dune slacks. *Journal of Vegetation Science,* 15, 449-456.

BOSSUYT, B., HONNAY, O. & HERMY, M. 2005. Evidence for community assembly constraints during succession in dune slack plant communities. *Plant Ecology,* 178, 201-209.

BRISTOW, C. 2003. *The impact of forestry on coastal geomorphology at Newborough Warren/Ynys Llanddwyn NNR, SSSI, pSAC. Final Report for Countryside Council of Wales, Volume 1*. London: University College London and Birkbeck College.

CHAFETZ, H.S. 1994. Bacterially induced precipitates of calcium carbonate and lithification of microbial mats. *In:* KRUMBEIN, W.E., PATERSON, D.M. & STAL, L.J. eds. *Biostabilization of Sediments*, 149-163. Oldenburg, Germany: BIS Verlag.

CLARKE, D. 1980. *Groundwater balance of a coastal sand dune system: a study of the water table in Ainsdale Sand Dunes N.N.R., Merseyside*. Liverpool: PhD thesis.

CLARKE, D. & PEGG, R.K. 1993. Hydrological investigations in the Ainsdale sand dunes National nature Reserve. *In:* ATKINSON, D. & HOUSTON, J. eds. *The Sand Dunes of the Sefton Coast*, 55-58. Liverpool: National Museums & Galleries on Merseyside.

CRANDALL-STOTLER, B.J., STOTLER, R.E. & FORD, C.H. 2002. Contributions toward a monograph of Petalophyllum (Marchantiophyta). *Novon*, 12, 334-337.

CRAWFORD, R.M.M. & WISHART, D. 1966. A multivariate analysis of development of dune slack vegetation in relation to coastal accretion at Tentsmuir Fife. *Journal of Ecology*, 54, 729-744.

DE BONT, A.J., and others. 1999. Vegetation development influenced by grazing in the coastal dunes near The Hague, The Netherlands. *Journal of Coastal Conservation*, 5, 59-68.

DENTON, J.S. & BEEBEE, T.J.C. 1997. Effects of predator interactions, prey palatability and habitat structure on survival of natterjack toad *Bufo calamita* larvae in replicated semi-natural ponds. *Ecography*, 20, 166-174.

DENTON, J.S., and others. 1997. A recovery program for the natterjack toad (*Bufo calamita*) in Britain. *Conservation Biology*, 11, 1329-1338.

EDMONDSON, S.E. 1 992. *Spatial and temporal variation in dune slack vegetation at Ainsdale National Nature Reserve, Merseyside*. University of Liverpool: PhD thesis.

EDMONDSON, S.E., and others. 1993. Plant communities and succession. *In:* ATKINSON, D. & HOUSTON, J. eds. *The Sand Dunes of the Sefton Coast*, 65-84. Liverpool: National Museums & Galleries on Merseyside.

ENTEC. 2003. *Eco-hydrological guidelines for lowland wetland plant communities*. Environment Agency.

ERNST, W.H.O. & PICCOLI, F. 1995. Fruit development and performance of *Schoenus nigricans* in coastal dune slacks of Europe - an extension of Baker, H.G. seed mass-altitude to a seed mass-latitude relationship. *Acta Botanica Neerlandica*, 44, 41-53.

ERNST, W.H.O., SLINGS, Q.L. & NELISSEN, H.J.M. 1996. Pedogenesis in coastal wet dune slacks after sod-cutting in relation to revegetation. *Plant and Soil*, 180, 219-230.

ERNST, W.H.O. & VAN DER HAM, N.F. 1988. Population structure and rejuvenation potential of *Schoenus nigricans* in coastal wet slacks. *Acta Botanica Neerlandica*, 37, 451-465.

EUROPEAN-COMMUNITIES. 2000. *Managing Natura 2000 sites: the provisions of Article 6 of the Habitats Directive 92/43/CEE*. Luxembourg: Office for Official Publications of the European Communities.

EUROPEAN COMMISSION DG ENVIRONMENT. 2003. *Interpretation manual of European Union habitats* (version EUR25). Brussels: European Commission DG Environment.

GEELEN, L.H.W., COUSIN, E.F.H. & SCHOON, C.F. 1995. Regeneration of dune slacks in the Amsterdam Waterworks Dunes. *In:* HEALY, M.G. & DOODY, J.P. eds. *Directions in European Coastal Management*, 525-532.

GITAY, H. & AGNEW, A.D.Q. 1989. Plant community structure, connectance, niche limitation and species guilds within a dune slack grassland. *Vegetatio*, 83, 241-248.

GONZÁLEZ BERNÁLDEZ, F., REY BENAYAS, J.M. & MARTÍNEZ, A. 1993. Ecological impact of groundwater extraction on wetlands (Douro Basin, Spain). *Journal of Hydrology*, 141, 219-138.

GORHAM, E. 1958. Soluble salts in dune sands from Blakeney point in Norfolk. *Journal of Ecology*, 46, 373-379.

GORHAM, E. 1961. The chemical composition of some waters from dune slacks at Sandscale, north Lancashire. *Journal of Ecology*, 49, 78-82.

GREIPSSON, S. 2002. Coastal dunes. *In:* PERROW, M.P. & DAVY, A.J. eds. *Handbook of Ecological Restoration. Vol. 2. Restoration in Practice*, 214-237. Cambridge: Cambridge University Press.

GROOTJANS, A.P., and others. 2004. Why young coastal dune slacks sustain a high biodiversity. *In:* MARTÍNEZ, A. & PSUTY, N.P. eds. *Coastal Dunes, Ecology and Conservation*, 85-101. Berlin: Springer-Verlag.

GROOTJANS, A.P., ERNST, W.H.O. & STUYFZAND, P.J. 1998. European dune slacks: strong interactions between vegetation, pedogenesis and hydrology. *Trends in Ecology and Evolution*, 13, 96-100.

GROOTJANS, A.P., and others. 2001. Restoration of wet dune slacks on the Dutch Wadden Sea islands: Recolonization after large-scale sod cutting. *Restoration Ecology*. 9, 137-146.

GROOTJANS, A.P., and others. 2002. Restoration of coastal dune slacks in the Netherlands. *Hydrobiologia*, 478, 181-203.

GROOTJANS, A.P., and others. 1991. Succession and fluctuation in a wet dune slack in relation to hydrological changes. *Journal of Vegetation Science*, 2, 545-554.

GROOTJANS, A.P., and others. 1988. Vegetation dynamics in a wet dune slack .1. Rare species decline on the Wadden-Island of Schiermonnikoog in the Netherlands. *Acta Botanica Neerlandica*, 37, 265-278.

GROOTJANS, A.P., LAMMERTS, E.J. & VAN BEUSEKOM, F., ed. 1995. *Kalkrijke duinvelleien op de Waddeneilanden*. Groningen, The Netherlands.

GROOTJANS, A.P., SIVAL, F.P. & STUYFZAND, P.J. 1996. Hydro-geochemical analysis of a degraded dune slack. *Vegetatio,* 126, 27-38.

GROOTJANS, A.P., VAN DER ENDE, F.P. & WALSWEER, A.F. 1997. The role of microbial mats during primary succession in calcareous dune slacks: an experimental aproach. *Journal of Coastal Conservation,* 3, 95-102.

HILL, T.G. & HANLEY, J.A. 1914. The structure and water content of shingle beaches. *Journal of Ecology,* 2, 21.

HOPE-SIMPSON, J.F. & YEMM, E.W. 1979. Braunton Burrows: developing vegetation in dune slacks, 1948-77. *In:* JEFFERIES, R.L. & DAVY, A.J. eds. *Ecological processes in coastal environments*, 113-127. Oxford: Blackwell Scientific Publications.

IMPACT ASSESSMENT UNIT, OXFORD BROOKES UNIVERSITY. 2002. *Assessment of plans and projects significantly affecting Natura 2000 sites*. Luxembourg: Office for Official Publications of the European Communities.

JAMES, P.A. & WHARFE, A.J. 1989. Timescales of soil development in a coastal sand dune system, Ainsdale, north-west England. *In:* VAN DER MEULEN, F., JUNGERIUS, P.D. & VISSER, J. eds. *Perspectives in coastal dune management*, 287-295. The Hague: SPB Academic Publishing.

JANNSON, M.P. & SALMAN, A.H.P.M. 1995. A national strategy for dune conservation in The Netherlands. *In:* SALMAN, A.H.P.M., BERENDS, H. & BONAZOUNTAS, M. eds. *Coastal Management and Habitat Conservation,* 215-230. Leiden: EUCC.

JONES, M.L.M., and others. 2002a. *Changing nutrient budget of sand dunes: Consequences for the nature conservation interest and dune management 2. Field survey*. Bangor, UK: Centre for Ecology and Hydrology.

JONES, M.L.M., and others. 2005. *Determining a nitrogen budget for Merthyr Mawr sand dune system: Final Report*. Bangor, UK: Centre for Ecology & Hydrology.

JONES, M.L.M., and others. 2002b. *Changing nutrient budgets of sand dunes: Consequences for the nature conservation interest and dune management. 1. A review*. Bangor, Centre for Ecology and Hydrology.

JONES, M.L.M., and others. 2004. Changes in vegetation and soil characteristics in coastal sand dunes along a gradient of atmospheric nitrogen deposition. *Plant Biology*, 6, 598-605.

JONES, P.S. 1993a. *Ecological and hydrological studies of dune slack vegetation at Kenfig NNR, Mid-Glamorgan*. University of Wales: PhD thesis.

JONES, P.S. 1993b. The importance of hydrological processes in sand dune ecosystems. *In:* ATKINSON, D. & HOUSTON, J. eds. *The Dunes of the Sefton Coast*, 59-62. Liverpool: National Museum and Galleries on Merseyside.

JONES, P.S. 1998. Aspects of the population biology of *Liparis loeselii* (L.) Rich. var. *ovata* Ridd. ex Godfery (Orchidaceae) in the dune slacks of South Wales, UK. *Botanical Journal of the Linnean Society*, 126, 123-139.

JONES, P.S. & ETHERINGTON, J.R. 1989. Ecological and physiological studies of sand dune slack vegetation, Kenfig Pool and Dunes local nature reserve, mid-Glamorgan, Wales, U.K. *In:* VAN DER MEULEN, F., JUNGERIUS, P.D. & VISSER, J. eds. *Perspectives in coastal dune management*, 297-303. The Hague, the Netherlands: SPB Academic Publishing.

JONES, P.S. & ETHERINGTON, J.R. 1992. Autecological studies on the rare orchid *Liparis loeselii* and their application to the management of dune slack ecosystems in South Wales. *In:* CARTER, R.W.G., CURTIS, T.G.F. & SHEEHY-SKEFFINGTON, M.J. eds. *Coastal Dunes: Geomorphology, Ecology and Management for Conservation*, 299-312. Rotterdam: A.A. Balkema.

JONES, R. 1972a. Comparative studies of plant growth and distribution in relation to waterlogging V. Uptake of iron and manganese by dune and dune slack plants. *Journal of Ecology*. 60, 131-139.

JONES, R. 1972b. Comparative studies of plant growth and distribution in relation to waterlogging VI. Effect of manganese on the growth of dune and dune slack plants. *Journal of Ecology*, 60, 141-145.

JONES, R. 1973. Comparative studies of plant growth and distribution in relation to waterlogging VII. Influence of water-table fluctuations on iron and manganese availability in dune slack soils. *Journal of Ecology*, 61, 107-116.

JONES, R. 1975a. Comparative studies of plant growth and distribution in relation to waterlogging IX. Uptake of potassium by dune and dune slack plants. *Journal of Ecology*, 63, 859-866.

JONES, R. 1975b. Comparative studies of plant growth and distribution in relation to waterlogging VIII. Uptake of phosphorus by dune and dune slack plants. *Journal of Ecology*, 63, 109-116.

JONES, R. & ETHERINGTON, J.R. 1971. Comparative studies of plant growth and distribution in relation to waterlogging IV. Growth of dune and dune slack plants. *Journal of Ecology*, 59, 793-801.

KENNOYER, G.J. & ANDERSON, M.P. 1989. Groundwater's dynamic role in regulating acidity and chemistry in a precipitation lake. *Journal of Hydrology,* 109, 287-306.

KENT, M., OWEN, N.W. & DALE, M.P. 2005. Photosynthetic responses of plant communities to sand burial on the machair dune systems of the Outer Hebrides, Scotland. *Annals of Botany*, 95, 869-877.

KOERSELMAN, W. 1992. The nature of nutrient limitation in Dutch dune slacks. *In:* CARTER, R.W.G., CURTIS, T.G.F. & SHEEHY-SKEFFINGTON, M.J. eds. *Coastal Dunes: Geomorphology, Ecology and Management for Conservation*, 189-199. Rotterdam: A.A. Ballkema.

KOOIJMAN, A.M. & BESSE, M. 2002. On the higher availability of N and P in lime-poor than in lime-rich coastal dunes in the Netherlands. *Journal of Ecology,* 90, 394-403.

KOOIJMAN, A.M. & DE HAAN, M.W.A. 1995. Grazing as a measure against grass encroachment in Dutch dry dune grassland: effects on vegetation and soil. *Journal of Coastal Conservation,* 1, 127-134.

LAMERS, L.P.M., TOMASSEN, H.B.M. & ROELOFS, J.G.M. 1998. Sulfate-induced eutrophication and phytotoxicity in freshwater wetlands. *Environmental Science and Technology,* 32, 199-205.

LAMMERTS, E.J. & GROOTJANS, A.P. 1997. Nutrient deficiency in dune slack pioneer vegetation: a review. *Journal of Coastal Conservation,* 3, 87-94.

LAMMERTS, E.J. & GROOTJANS, A.P. 1998. Key environmental variables determining the occurrence and life span of basiphilous dune slack vegetation. *Acta Botanica Neerlandica*, 47, 369-392.

LAMMERTS, E.J., GROOTJANS, A.P., STUYFZAND, P.J. & SIVAL, F.P. 1995. Endangered dune slack gastronomers in need of mineral water. *In:* SALMAN, A.H.P.M., BERENDS, H. & BONAZOUNTAS, M. eds. *Coastal management and habitat conservation*, Leiden, the Netherlands: EUCC.

LAMMERTS, E.J., MAAS, C. & GROOTJANS, A.P. 2001. Groundwater variables and vegetation in dune slacks. *Ecological Engineering,* 17, 33-47.

LAMMERTS, E.J., and others. 1999. Nutrient limitation and vegetation changes in a coastal dune slack. *Journal of Vegetation Science,* 10, 111-122.

LAMMERTS, E.J., and others. 1992. Hydrological conditions and soil buffering processes controlling the occurence of dune slacks species on the Dutch Wadden Sea. *In:* CARTER, R.W.G., CURTIS, T.G.F. & SHEEHY-SKEFFINGTON, M.J. eds. *Coastal dune: Geomorphology, Ecology and Management for Conservation*, 265-281. Rotterdam, the Netherlands: A.A. Balkema.

LONDO, G. 1971. *Pattern and process in dune slack vegetation along an excavated lake in the Kennemer dunes (the Netherlands*. Nijmegen: PhD thesis.

LUCAS, N.S., SHANMUGAM, S. & BARNSLEY, M. 2002. Sub-pixel habitat mapping of a coastal dune ecosystem. *Applied Geography*, 22, 253-270.

MALCOLM, R. & SOULSBY, C. 1998. The impact of climate change on a restored coastal wetland in north-east Scotland. *In:* eds. *Proceedings of the Second International Conference on Climate and Water, Vols 1-3*, 543-552. Espoo 15: Hesinki University Technology.

MALCOLM, R. & SOULSBY, C. 2001. Hydrogeochemistry of groundwater in coastal wetlands: implications for coastal conservation in Scotland. *Science of the Total Environment*, 265, 269-280.

MARTÍNEZ, A. & PSUTY, N.P., ed. 2004. *Coastal dunes, ecology and conservation*. Berlin: Springer-Verlag.

MAY, V.J. 2003. Sandy beaches and dunes - GCR reports. *In:* MAY, V.J. & HANSOM, J.D. eds. *Coastal geomorphology of Breat Britain: Geological Conservation Review Series No. 28*, 327-413. Peterborough: JNCC.

MAY, V.J. & HANSOM, J.D., ed. 2003. *Coastal geomorphology of Breat Britain: Geological Conservation Review Series No. 28*. Peterborough: Joint Nature Conservation Committee.

MCLEOD, C.R., and others. 2002. *The Habitats Directive: selection of Special Areas of Conservation in the UK*. Peterborough: Joint Nature Conservation Committee.

MOUNTFORD, J.O., ROSE, R.J. & BROMLEY, J. 2005. *Eco-hydrological guidelines for wet heath - Phase I. English Nature Research Reports 620*. Peterborough: English Nature.

MUNOZ-REINOSO, J.C. 2001a. Sequential pattern in the stabilized dunes of Doñana Biological Reserve (SW Spain). *Journal of Coastal Research*, 17, 90-94.

MUNOZ-REINOSO, J.C. 2001b. Vegetation changes and groundwater abstractions on S.W. Doñana. *Journal of Hydrology*, 242, 197-209.

MUNOZ-REINOSO, J.C. & DE CASTRO, F. 2005. Application of a statistical water-table model reveals connections between dunes and vegetation at Doñana. *Journal of Arid Environments*, 60, 663-679.

MUNOZ-REINOSO, J.C. & GARCIA NOVO, F. 2005. Multiscale control of vegetation patterns: the case of Doñana (SW Spain). *Landscape Ecology*, 20, 51-61.

NOEST, V. 1991. Simulated impact of sea-level rise on phreatic level and vegetation of dune slacks in the Voorne dune area (the Netherlands). *Landscape Ecology*, 6, 89-97.

OLFF, H., and others. 1997. Vegetation succession and herbivory in salt marshes: changes induced by sea level rise and silt deposition along an elevation gradient. *Journal of Ecology*, 85, 799-814.

OLFF, H., HUISMAN, J. & VAN TOOREN, B.F. 1993. Species dynamics and nutrient accumulation during early primary succession in coastal sand dunes. *Journal of Ecology*, 81, 693-706.

ONYEKWELU, S.S.C. 1972a. The vegetation of dune slacks at Newborough Warren. I. Ordination of the vegetation. *Journal of Ecology*, 60, 887-898.

ONYEKWELU, S.S.C. 1972b. The vegetation of dune slacks at Newborough Warren. III. *Plantago coronopus*. *Journal of Ecology*, 60, 907-915.

OWEN, N.W., KENT, M. & DALE, D.M. 2004. Plant species and community responses to sand burial on the machair of the Outer Hebrides, Scotland. *Journal of Vegetation Science*, 15, 669-678.

PACKHAM, J.R. & WILLIS, A.J. 1997. *Ecology of dunes, salt marsh and shingle*. London: Chapman & Hall.

PERROW, M.R. & DAVY, A.J. 2002a. *Handbook of Ecological Restoration Volume 1: Principles of Restoration*. Cambridge: Cambridge University Press.

PERROW, M.R. & DAVY, A.J. 2002b. *Handbook of Ecological Restoration Volume 2: Restoration in Practice*. Cambridge: Cambridge University Press.

PETANIDOU, T., and others. 1998. Pollination ecology of *Gentianella uliginosa*, a rare annual of the Dutch coastal dunes. *Nordic Journal of Botany*, 18, 537-548.

PETERSEN, J. 2000. *Die Dünentalvegetation der Wattenmeer-Inseln in der südlichen Nordsee. Eine pflanzensociologische und ökologische Vergleichsuntersuchung unter Berücksichtigung von Nutzung and Naturschutz*. University of Hannover: PhD thesis.

PIOTROWSKA, H. 1988. The dynamics of the dune vegetation of the Polish Baltic coast. *Vegetatio*, 77, 169-175.

PLUIS, J.L.A. & DE WINDER, B. 1990. Natural stabilization. *In:* BAKKER, T.W.M., JUNGERIUS, P.D. & KLIJN, J.A. eds. *Dunes of the European coasts*, 195-208. Cremlingen-Destedt: CATENA-verlag.

PRUMMEL, W. & HEINRICH, D. 2005. Archaeological evidence of former occurrence and changes in fishes, amphibians, birds, mammals and molluscs in the Wadden Sea area. *Helgoland Marine Research*, 59, 55-70.

PYE, K. & SAYE, S. 2005. *The geomorphological response of Welsh sand dunes to sea level rise over the next 100 years and the management implications for SAC and SSSI sites. Final Report for Countryside Council for Wales*. Crowthorne, Berkshire: Kenneth Pye Associates Ltd.

RADLEY, G.P. 1994. *Sand dune vegetation survey of Great Britain: Part 1- England*. Peterborough: Joint Nature Conservation Committee.

RANWELL, D. & BOAR, R. 1986. *Coast dune management guide*. Abbots Ripton, Huntingdon, UK: Institute for Terrestrial Ecology.

RANWELL, D.S. 1959. Newborough-Warren, Anglesey I. The dune system and dune slack habitat. *Journal of Ecology,* 47, 571-601.

RANWELL, D.S. 1960a. Newborough Warren, Anglesey II. Plant associes and succession cycles of the sand dune and dune slack vegetation. *Journal of Ecology,* 48, 117-141.

RANWELL, D.S. 1960b. Newborough Warren, Anglesey III. Changes in the the vegetation on parts of the dune system after the loss of rabbits by myxomatosis. *Journal of Ecology,* 48, 385-395.

RANWELL, D.S. 1972. *Ecology of salt marshes and dunes*. London: Chapman & Hall.

RODWELL, J.S., ed. 2000. *British plant communities, Volume 5: Maritime communities and vegetation of open habitats*. Cambridge: Cambridge University Press.

SALISBURY, E.J. 1952. *Downs and dunes*. London: Bell.

SCHAT, H. 1983. Germination ecology of some dune slack pioneers. *Acta Botanica Neerlandica,* 32, 203-212.

SCHAT, H. 1984. A comparative ecophysiological study on the effects of waterlogging and submergence on dune slack plants - growth, survival and mineral nutrition in sand culture experiments. *Oecologia*, 62, 279-286.

SCHAT, H., BOS, A.H. & SCHOLTEN, M. 1984. The mineral nutrition of some therophytes from oligotrophic dune slack soils. *Acta Oecologica, Oecologia Plantarum*. 5, 119-131.

SCHAT, H. & SCHOLTEN, M. 1985. Comparative population ecology of dune slack species - the relation between population stability and germination behavior in brackish environments. *Vegetatio*. 61, 189-195.

SIVAL, F.P. 1996. Mesotrophic basiphilous communities affected by changes in soil properties in two dune slack chronosequences. *Acta Botanica Neerlandica,* 45, 95-106.

SIVAL, F.P. & GROOTJANS, A.P. 1996. Dynamics of seasonal bicarbonate supply in a dune slack: Effects on organic matter, nitrogen pool and vegetation succession. *Vegetatio,* 126, 39-50.

SIVAL, F.P., and others. 1997. Variation in groundwater composition and decalcification depth in a dune slack: Effects on basiphilous vegetation. *Journal of Coastal Conservation*, 3, 79-86.

SIVAL, F.P., MÜCHER, H.J. & VAN DELFT, S.P.J. 1998. Management of basiphilous dune slack communities in relation to carbonate accumulation and hydrological conditions. *Journal of Coastal Conservation*, 4, 91-100.

SIVAL, F.P. & STRIJKSTRA-KALK, M. 1999. Atmospheric deposition of acidifying and eutrophicating substances in dune slacks. *Water Air and Soil Pollution*,116, 461-477.

SMITH, P.H. 2006a. Changes in the floristic composition of sand-dune slacks over a twenty-year period. *Watsonia*, 26, 41-49.

SMITH, P.H. 2006b. Revisiting *Juncus balticus* Willd. in England. *Watsonia*, 26, 57-65.

SNOWDEN, R.E.D. & WHEELER, B.D. 1993. Iron toxicity to fen plant species. *Journal of Ecology*, 81, 35-46.

SOULSBY, C., and others. 1997. Hydrogeology of a restored coastal dune system in northeastern Scotland. *Journal of Coastal Conservation*, 3, 143-154.

STAL, L.J., VILLBRANDT, M. & DE WINDER, B. 1994. Nitrogen fixation in microbial mats. *In:* KRUMBEIN, W.E., PATERSON, D.M. & STAL, L.J. eds. *Biostabilisation of sediments*, 384-399. Oldenburg, Germany: BIS Verlag.

STEERS, J.A. & JENSEN, H.A.P. 1953. Winterton Ness. *Transactions of the Norfolk and Norwich Naturalists' Society*, 17, 259-274.

STEVERS, R.A.M. 1986. Restoration of wet dune slack ecosystems in the heavily affected dune areas of Meijendel and Berkheide. *Acta Botanica Neerlandica*, 35, 124-124.

STEWART, W.D.P. 1967. Transfer of biologically fixed nitrogen in a sand dune slack region. *Nature*, 214, 603-&.

STUDER-EHRENSBERGER, K., STUDER, C. & CRAWFORD, R.M.M. 1993. Competition at community boundaries: mechanisms of vegetation structure in a dune slack complex. *Functional Ecology*. 7, 156-168.

STURGESS, P.W. 1993. Clear-felling dune plantations: studies in vegetation recovery on the Sefto Coast. *In:* ATKINSON, D. & HOUSTON, J. eds. *The Sand Dunes of the Sefton Coast*, 85-89. Liverpool: National Museums & Galleries on Merseyside.

STUYFZAND, P.J. 1993. *Hydrochemistry and hydrology of the coastal dune area of the western Netherlands*. Free University of Amsterdam: PhD thesis.

SYKORA, K.V., VAN DEN BOGERT, J.C.J.M. & BERENDSE, F. 2004. Changes in soil and vegetation during dune slack succession. *Journal of Vegetation Science*. 15, 209-218.

TANSLEY, A.G. 1949. *The British Islands and their vegetation*. London: Cambridge University Press.

TEN HARKEL, M.J. & VAN DER MEULEN, F. 1996. Impact of grazing and atmospheric deposition on the vegetation of dry coastal dune grasslands. *Journal of Vegetation Science,* 7, 445-452.

TER HEERDT, G.N.J., SCHUTTER, A. & BAKKER, J.P. 1999. The effect of water supply on seed-bank analysis using the seedling-emergence method. *Functional Ecology*. 13, 428-430.

THOMPSON, K., BAKKER, J.P. & BEKKER, R.M. 1997. *Soil seed banks of North West Europe*. Cambridge: Cambridge University Press.

THOMSON, A.G. 1995. Airborne radiometry and a sheep grazing experiment on dune grassland. *International Journal of Remote Sensing*, 16, 981-988.

VAN ANDEL, J., BAKKER, J.P. & GROOTJANS, A.P. 1993. Mechanisms of vegetation succession - a review of concepts and perspectives. *Acta Botanica Neerlandica,* 42, 413-433.

VAN BECKHOVEN, K. 1992. Effects of groundwater manipulation on soil processes and vegetation in wet dune slacks. *In:* CARTER, R.W.G., CURTIS, T.G.F. & SHEEHY-SKEFFINGTON, M.J. eds. *Coastal dune: Geomorphology, Ecology and Management for Conservation,* 251-263. Rotterdam, the Netherlands: A.A. Balkema.

VAN BECKHOVEN, K. 1995. *Rewetting of coastal duneslacks: effects on plant growth and soil processes*. Free University of Amsterdam: PhD thesis.

VAN BODEGOM, P.M., DE KANTER, M., BAKKER, C. & AERTS, R. 2005. Radial oxygen loss, a plastic property of dune slack plant species. *Plant and Soil,* 271, 351-364.

VAN DER MAAREL, E., BOOT, R.G.A., VAN DORP, D. & RIJNTJES, J. 1985. Vegetation succession on the dunes near Oostvoorne, The Netherlands: a comparison of the vegetation in 1959 and 1980. *Vegetatio,* 58, 137-187.

VAN DER MAAREL, E. & VAN DER MAAREL-VERSLUYS, M. 1996. Distribution and conservation status of littoral vascular plant species along the European coasts. *Journal of Coastal Conservation,* 2, 73-92.

VAN DER MEULEN, F. 1990. Geohydrology of coastal dunes. *In:* BAKKER, T.W.M., JUNGERIUS, P.D. & KLIJN, J.A. eds. *Dunes of the European Coasts,* 209-223. Cremlingen-Destedt: CATENA-Verlag.

VAN DIJK, H.W.J. 1986. Chemical aspects concerning wet dune slack regeneration. *Acta Botanica Neerlandica*, 35, 123-123.

VAN DIJK, H.W.J. 1989. Ecological impact of drinking-water production in Dutch coastal dunes. *In:* VAN DER MEULEN, F., JUNGERIUS, P.D. & VISSER, J. eds. *Perspectives in coastal dune management*, 163-182. The Hague, the Netherlands: SPB Academic Publishing.

VAN DIJK, H.W.J. 1992. Grazing domestic livestock in Dutch coastal dunes: experiments, experiences and perspectives. *In:* CARTER, R.W.G., CURTIS, T.G.F. & SHEEHY-SKEFFINGTON, M.J. eds. *Coastal dune: Geomorphology, Ecology and Management for Conservation,* 235-250. Rotterdam, the Netherlands: A.A. Balkema.

VAN DIJK, H.W.J. & GROOTJANS, A.P. 1993. Wet dune slacks: decline and new opportunities. *Hydrobiologia*. 265, 281-304.

VAN GEMERDEN, H. 1993. Microbial mats: a joint venture. *Marine Geology*, 113, 3-25.

VAN WIJNEN, H. 1999. *Nitrogen dynamics and vegetation succession in salt marshes*. Groningen: PhD thesis.

VAZQUEZ, G., MORENO-CASASOLA, P. & BARRERA, O. 1998. Interaction between algae and seed germination in tropical dune slack species: a facilitation process. *Aquatic Botany,* 60, 409-416.

VEER, M.A.C. 1997. Nitrogen availability in relation to vegetation changes resulting from grass encroachment in Dutch dry dunes. *Journal of Coastal Conservation,* 3, 41-48.

VERHOEVEN, J.T.A., KOERSELMAN, W. & MEULEMAN, A.F.M. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: realtions eith atmospheric inputs and management regimes. *Trends in Ecology and Evolution,* 11, 494-496.

WESTHOFF, V. & VAN OOSTEN, M. 1991. *De plantengroei van de Waddeneilanden*. Utrecht: KNNV.

WHEELER, B.D., and others. 2004. *Ecohydrological guidelines for lowland wetland plant communities*. Peterborough: Environment Agency (Anglian Region).

WHEELER, B.D., LAMBLEY, P.W. & GEESON, J. 1998. *Liparis loeselii* (L.) Rich. in eastern England: constraints on distribution and population development. *Botanical Journal of the Linnean Society.* 126, 141-158.

WHEELER, B.D., MONEY, R.P. & SHAW, S.C. 2002. Freshwater wetlands. *In:* PERROW, M.P. & DAVY, A.J. eds. *Handbook of Ecological Restoration. Vol. 2. Restoration in Practice*, 325-354. Cambridge: Cambridge University Press.

WHEELER, B.D. & SHAW, S.C. 2000. *A wetland framework for impact assessment at statutory sites in eastern England. R&D Technical Report W6-068/TR1*. Bristol: Environment Agency.

WHEELER, B.D. & SHAW, S.C. 2001. *A wetland framework for impact assessment at statutory sites in eastern England: Site accounts. R&D Technical Report W6-068/TR2*. Bristol: Environment Agency.

WILLIS, A.J. 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. *Journal of Ecology*m, 51, 353-374.

WILLIS, A.J. 1985a. Dune water and nutrient regimes - their ecological relevance. *In:* DOODY, P. eds. *Sand dunes and their management*, 159-174. Peterborough: Nature Conservancy Council.

WILLIS, A.J. 1985b. Plant diversity and change in a species-rich dune system. *Transactions of the Botanical Society of Edinburgh*, 44, 291-308.

WILLIS, A.J., FOLKES, B.F., HOPE-SIMPSON, J.F. & YEMM, E.W. 1959a. Braunton Burrows: the dune system and its vegetation. Part I. *Journal of Ecology,* 47, 1-24.

WILLIS, A.J., and others. 1959b. Braunton Burrows: the dune system and its vegetation. Part II. *Journal of Ecology*, 47, 249-288.

WILLIS, A.J. & YEMM, E.W. 1961. Braunton Burrows: mineral nutrient status of the soils. *Journal of Ecology,* 49, 377-390.

ZOLADESKI, C.A. 1991. Vegetation zonation in dune slacks on the Lebra Bar, Polish Baltic sea coast. *Journal of Vegetation Science*, 2, 255-258.

ZONNEVELD, L.M.L. 1992. Ecohydrological dune slack research for management purposes. *In:* eds. *Coastal Dunes: Geomorphology, Ecology and Management for Conservation*, 397-406. Rotterdam: A.A. Balkema.

ZUNZUNEGUI, M., DIAS BARRADAS, M. & GARCÍA NOVO, F. 1 998. Vegetation fluctuation in Mediterranean dune ponds in relation to rainfall variation and water extraction. *Applied Vegetation Science*, 1, 151-160.

8 Groups known to be working on dune slacks

Dr M.L.M. Jones and colleagues Centre for Ecology and Hydrology Orton Building UWB Deionol road Bangor LL572UP	Nitrogen budgets of dune systyems and critical loads for nitrogen deposition
Dr. Peter van Bodegom Chris Bakker (until Jan 2005) Free University of Amsterdam Institute of Ecological Science. Dept of Systems Ecology De Boelelaan 1085 NL-1081 HV Amsterdam The Netherlands http://www.falw.vu.nl/iew/systeco/	He has finished a 4 year project on rewetting of dune slacks along the Dutch main coast (National Park Zuid-Kennemerland), after the elimination of a drinking water plant. A PhD thesis on dune slack regeneration (C. Bakker) has just been published.
Prof. Pieter Stuyfzand Free University Amsterdam and KIWA research Institute Niewegein. P.O.Box 1072 3430 BB Nieuwegein The Netherlands	He is a hydrologist at Amsterdam, but is mainly working for a commercial company. Is a hydrologist and hydrogeochemist for water companies on the pollution of dune slacks.
Dr. Bea Bossuyt and Prof Martin Hermy University of Leuven Belgium	They have worked on vegetation succession, seed banks, and dispersal in Belgium dune slacks (Bossuyt and Hermy 2004; Bossuyt and others 2005). He has applied for a new grant on eco-hydrology of dune slacks, but result not known.
Dr. Maria Luisa Martinez Departamento de Ecología Vegetal Instituto de Ecología, A.C. km 2.5 antigua carretera a Coatepec Xalapa, Ver. 91000 Mexico	She works with a group in Dunes and Dune wetlands and has recently edited a Springer book (Ecological Studies 171) on Coastal Dunes. (Martínez and Psuty 2004)
Fiona Devaney and Dr. Marinus Otte Department of Botany, UCD, Ireland Marinus L Otte marinus.otte@ucd.ie	Fiona is preparing a PhD thesis on the eco-hydrology of Dune slacks.
Prof. Francisco Garcia-Novo University of Sevilla Apartado 1095 E41050 Sevilla Spain fgnova@us.es	He is working with a team on the Coto Doñana dunes; also on the hydrology of dune wetlands and the impact of groundwater abstraction facilities for tourist resorts.

Dr Jörg Petersen University of Hannover/Germany Nature-Consult, Fachbüro für Vegetationsökologie, Hydrogeologie und Naturschutz Management, Hackelbrink 21, D-31139 Hildesheim, Germany www.nature-consult.de/html/home.html)	He has completed a thesis on all the Dutch Danish and German Wadden Sea islands. He is a vegetation scientist, who has described all dune slacks in that area and made many measurements of pH and organic matter content in dune-slack soils.
Annemiek Kooijmans/Bas Arends University of Amsterdam Private address Annemiek: Klooster 12 2871 BJ Schoonhoven The Netherlands	Annemiek is coordinating research aimed at monitoring restoration activities in dry coastal dunes. She has a focus on mineralisation and grass encroachment. Bas finished a thesis on geomorphology of the fore-dunes and wind blown dunes and now has his own firm that focuses on dynamics of dune geomorphology.
Prof Martin Diekman and Maike Isermann, University of Bremen Germany	They are working on dune species (Maike on *Hippophae rhahmnoides*) and also rare species (*Parnassia palustris*) of dune slacks.
Prof Peter Janiesch University of Oldenburg Institut für Biologie und Umweltwissenschaften (IBU) Pflanzenökologie D-26111 Oldenburg Germany	He has done some work in dunes slack on the German Wadden Sea islands in cooperation with Jörg Pedersen (University of Hannover). At the moment there are no specific dune projects.
Ab Grootjans University of Groningen Community and Conservation Ecology Group. The Netherlands	

Appendix 1 Comparative typology of British and Wadden Island dune-slack communities

(NB: a colour copy of this table is in the pdf version of this report)

	Centaurio-	**pioneer stage**			**Parn**	**Junco baltici**					**Caricion davallianae**			
	Saginetum				**Junc**	**Schoenetum**								
					atric	**nigricantis**								
	Wad	UK	UK		NL	NL	WadNL	WadDK	UK	UK	UK	UK	UK	UK
	Petersen	Rodwell	Rodwell		Scham	Scham	Petersen	Petersen	Rodwell	Rodwell	Rodwell	Rodwell	Rodwell	Rodwell
		SD13a	SD13b		A6	A7	NL+Bork	GER/DK	SD14c	SD14d	SD14a	SD14b	SD16c	SD16d
nr of relevees	69	28	20		23	159	170	42	34	57	70	85	58	31
Samolus valerandi	+	I	I		I	I	I		I		I			
Sagina nodosa	V	V	IV		II	I	I	+	I		I		I	I
Centaurium littorale	V				III	I	I	II						
Centaurium pulchellum	II					+	+				I			
Centaurium erythraea		III	III											
Leontodon hispidus	II	IV	V			II			IV	II	II	I		
Aneura pinguis		V	V			I	+		IV	I	I	I		
Bryum pseudotriquetrum		V	V			I	+	I	V	I	I	I		
Moerckia hibernica		III	I		I				II	I	I		I	
Schoenus nigricans					III	IV	IV	II						
Gymnadenia conopsea						+	+		I	I				
Blackstonia perfoliata		III	I		+				I		I			
Liparis loeselii					I	II	II		I		I	I		
Pyrola rotundifolia		I	III			I		III	I	I			III	I
Eleocharis quinqueflora					I	II	I/II		I		I	I	I	I
Gentianella amarella					I	I	+		I	I			I	I
Parnassia palustris	+				V	IV	IV	IV	I	I				I
Dactylorhiza incarnata			I		I	II/IIII	I/II			I			I	II
Epipactis palustris	r		II		II	III	III	IV	IV	IV	II	V	I	II
Carex flacca	I	I	II		IV	III	IV	IV	V	V	III	V	V	V
Campylium stellatum		II	I			I	II	+	V	IV	V	V	II	II
Equisetum variegatum		I	III			I	+		IV	V	IV	V	IV	II
Anagallis tenella						+	+		II	I	I	I	I	II
Pellia endiviifolia		I	I		I	II	II	III	IV	II	I	I	II	I
Carex oederi	II	I	I		IV	III	III	III	II	I	III	I	I	II
Pedicularis palustris						II								
Linum catarticum	I				III	II	II/III	IV	III	I	I	I	II	I

Carex nigra									I	I	I	II		I
Calliergonella cuspidata	r				I		IV	V	IV	V	III	IV	II	II
Hydrocotyle vulgaris	r	III	II		II		IV	II	IV	V	V	V	II	III
Potentilla palustris														
Caltha palustris														
Lychnis flos-cuculi														
Filipendula ulmaria														
Dactylorhiza maj/purp						+					I			
Dactylorhiza maj/praet						+			I	I	I	I		
Dactylorhiza fuchsii														
Odontitus vernus	III						I							
Plantago maritima	II						+							
Glaux maritima	II				II	II	I	+	I	I	I	I		
Juncus gerardii	II				II	II	I	+		I	I	I		
Juncus alpinoarticulatus	II				V	III	III	II						
Juncus articus/balticus					I	I								
Carex trinervis					I	III	II							
Calamagrostis epigejos	r				II	III	III	II						
Juncus articulatus	II	IV	IV		IV	IV	IV	II	IV	II	III	III	I	III
Agrostis stolonifera	V	III	IV		V	IV	IV	II	V	IV	III	V	II	V
Salix repens	II	V	V		IV	V	V	V	V	V	V	V	V	V
Potentilla anserina	III				III	III	IV	II	I	II	II	II	I	I
Holcus lanatus		II	V		II	II	III	IV	III	IV	I	I	V	III
Lotus corniculatus	II		IV		I	I	I	I	V	IV	I	III	IV	V
Equisetum palustre		I	I		I	I			I	II	I	II	I	I
Equisetum fluviatile					I					I	I	I		
		SD13a	SD13b		NL	NL	WadNL	WadDK	SD14c	SD14d	SD14a	SD14b	SD16c	SD16d
Lowest water level (cm)		60-160	60-160		Scham	Scham	Petersen	Petersen	no info			no info	50-200	
Flooding frequency		less then	160 days		NL	NL	NL+Bork	GER/DK	regular flooding, not long				almost no flooding	

				dune slack types							Caricetum trinervi nigrae	
	UK	UK	UK	UK	UK	UK	UK	UK	UK	UK	NL	Wad
	Rodwell	Rodwell	Rodwell	Rodwell	Rodwell	Rodwell	Rodwell	Rodwell	Rodwell	Rodwell	Scham	Petersen
	SD16a	SD16b	SD15c	SD15b	SD15a	SD15d	SD17b	SD17d	SD17c	SD17a	A1	5.1
nr of relevees	67	47	48	57	81	33	32	46	40	24	48	235
Samolus valerandi			I			I						
Sagina nodosa	I	I										
Centaurium littorale												
Centaurium pulchellum												
Centaurium erythraea												
Leontodon hispidus												
Aneura pinguis												
Bryum pseudotriquetrum											+	
Moerckia hibernica												
Schoenus nigricans											+	
Gymnadenia conopsea												
Blackstonia perfoliata												
Liparis loeselii												
Pyrola rotundifolia	I	I										
Eleocharis quinqueflora											+	
Gentianella amarella	I											
Parnassia palustris				I			I			I	+	
Dactylorhiza incarnata	I	I					I	I	I		+	
Epipactis palustris	II	II	IV	III	I	I	II				+	+
Carex flacca	II	III	V	III	I	III	IV	I	I	I		+
Campylium stellatum	I	I	I	I	I			I			I	
Equisetum variegatum	I	I	V	IV	I	I	I	III				
Anagallis tenella		I	I	I		I						
Pellia endiviifolia												
Carex oederi	I	I									I	
Pedicularis palustris								I	II		II	+
Linum catarticum	II	I		I			I		I	I		
Carex nigra	I	I	II	III	IV	II	IV	V	V	III	III	V
Calliergonella cuspidata		I	V	V	V	V	V	IV	IV	IV	III	II

Hydrocotyle vulgaris		II	V	V	V	III	III	V	I	I	IV	IV
Potentilla palustris								I	I		IV	II
Caltha palustris				I	I		I	I	IV	II		
Lychnis flos-cuculi				I	I	I	I	I	III			
Filipendula ulmaria			I	I	I	I		I	I	I		
Dactylorhiza maj/purp							I	I	I			
Dactylorhiza maj/praet			I	I	I							
Dactylorhiza fuchsii									I			
Odontitus vernus							I			I		
Plantago maritima							II		I	I		
Glaux maritima									I	II		
Juncus gerardii												
Juncus alpinoarticulatus											III	I
Juncus articus/balticus											I	
Carex trinervis											V	II
Calamagrostis epigejos											III	III
Juncus articulatus	I	I	I	I	I	I	II	II	II	II	II	II
Agrostis stolonifera	II	II	IV	IV	II	II	III	IV	III	V	III	II
Salix repens	V	V	V	V	V	V	I	III			V	IV
Potentilla anserina	I	II	II	III	II	I	IV	IV	IV	V	II	
Holcus lanatus	IV	V	II	I	I	IV	III	I	IV	II	I	
Lotus corniculatus	IV	III	I	I		II	II					
Equisetum palustre		I	II	II	IV	IV	II	II	II	I	+	
Equisetum fluviatile								I	II		I	+
	SD16a	SD16b	SD15c	SD15b	SD15a	SD15d	SD17b	SD17d	SD17c	SD17a		
Lowest water level (cm)	measured		5-40 (estimate)				no info					
Flooding frequency			prolonged flooding				regular flooding					
			(up to 8 months)									

Appendix 2 Vulnerability of groundwater-fed dune slacks on the Dutch Wadden Sea islands

Introduction

Young dune-slacks are rare and highly valued for nature conservation since they are very species rich and harbour a large number of wetland species that have become endangered in most of the NW European lowland area. Some species are now restricted to the coastal area because all inland populations have become extinct due to severe drainage and fertilization. Examples are *Schoenus nigricans*, *Parnassia palustris*, *Epipactis palustris*, *Dactylorhiza incarnata*, *Herminium monorchis* and *Liparis loeselii*.

Fixation of the dunes led to an ongoing succession. This process was accelerated by atmospheric deposition from industrial areas and other human activities such as drainage and production of drinking water. Young dune-slacks turned into *Salix*-dominated shrub lands or into communities characteristic of acid soils such as heathland. Nowadays the more mature stages (shrub and forest) prevail in wet dune-slacks and the pioneer stages have become rare.

In the following we will shortly describe the history of groundwater abstraction along the Dutch Coast and its consequences for the remaining dune-slacks. We will also present one case study on the Wadden Sea islands of Schiermonnikoog, where much eco-hydrological research has been carried out in the framework of a large project aimed at finding solutions for the conflict between drinking water supply and nature conservation.

In the Netherlands, dune areas have been used for the production of drinking water since 1853 (Geelen and others 1995). Dune-slacks along the Dutch coast, in particular, have been very negatively affected by groundwater abstraction in since the 1950s due to the growing demand for drinking water from the large Dutch cities (Amsterdam, Rotterdam, The Hague). When most of the wet dune-slacks had severely dried out, due to lack of groundwater supply, a new technique to produce drinking water was introduced from 1957. Large amounts of surface water from the large rivers Rhine and Meuse were transported to the dunes and artificial recharge with purified river water was practised for almost 30 years. Due to the unnatural hydrological regime and the high flow rates with (slightly) polluted water, only very eutrophic plant communities (*Urtica dioica*, *Phragmites australis*, *Eupatorium cannabinum*) gained dominance in most slacks and mesotrophic dune-slack communities did not recover, despite a considerable rewetting (van Dijk and Grootjans 1993). Nowadays water companies are shifting towards a system of deep infiltration of purified surface water. This technique has little effect on surface hydrology and large restoration projects are being carried out at the moment, at great costs (one project near Amsterdam costs close to 1,000,000 euros). Between 1980 and 1995 nutrient conditions in affected dune-slacks (van Dijk and Grootjans 1993) and hydrological systems of the Dutch coastal area have been studied in great detail (Bakker 1990; Stuyfzand 1993) and provides a scientific background for eco-hydrological studies in the much less affected dune-slacks on the Dutch Wadden Sea islands.

Disputes about drinking water abstraction and nature conservation were most intense during the early 1990s. Some water companies decided to stop abstraction in dune areas due to various reasons; including political pressure from provincial authorities (one rumour was that on the Island of Texel a nearby camping site with leaking toilet facilities had polluted the well field). Drinking water from the mainland is now transported through a pipe line to two islands (Texel and Terschellling). On two smaller islands, Vlieland and Schiermonnikoog, the aim was to find new production techniques that were less harmful to the nature conservation value of dune-slacks that were within the influence of abstraction facilities.

Case study island of Schiermonnikoog

1976-1988: Assessing the damage

A pumping station for public water supply was installed in 1950 to the west and near (0.6 km) a dune-slack. The groundwater abstraction increased from 8,000 in 1950 to 150,000 m^3/year in 1988. In the nearby dune-slack complex (Kapenglop) changes in the vegetation composition were observed in a monitoring grid that had already been placed in 1964 by the University of Groningen, where the late Prof Dingeman Bakker of the Department of Ecology had anticipated changes in the hydrology. The dune-slack Kapenglop is situated in the central (and oldest) part of the island and is enclosed by three dune ridges of different ages (150-400 years). Originally the slack was a sandy beach plain. Some hundred years ago the flooding of sea water was prevented by the enclosure of the dune masses. From that time the dune-slack was influenced by freshwater from the central parts of the island. Wind blowing in the first half of the 20th century has altered the original geomorphology and created a mosaic of valleys and small dunes with heights up to 3 m. Pine trees were planted in the eastern part in 1912. Removing organic material by sod cutting occurred until the early 1960s in the western part of the dune-slack. Well developed stands of the *Samolo-Littorelletum* and the *Junco baltici-Schoenetum nigricantis* were observed here between 1952-1954. Practically all basiphilous species, such as *Schoenus nigricans*, *Dactylorhiza incarnata*, *Epipactis palustris* and *Pedicularis palustris* disappeared between 1977 and 1983. These changes were related to changes in the local hydrological system (groundwater abstraction) and not to decalcification of the top soil during that period (Grootjans and others 1991).

Preliminary hydrological model studies indeed showed that abstraction of groundwater had a significant effect on the hydrology of the slack, but it was not the only cause of the decline of the typical dune-slack species. Human interferences with the hydrology consisted of: (i) pumping of groundwater at a depth of 20-30 m below the surface in the western part of the island and (ii) lowering of the water table in the southern infiltration areas close to the top of the freshwater lens. In addition, mature pine plantations and the general development of shrub vegetation in the surroundings both increased evapotranspiration rates in the whole area.

1988 Start of the project 'Integrated water resources management Schiermonnikoog'

A project was initiated in 1988 in which all parties involved in the use of groundwater discussed possible measures to improve the hydrological condition for nature development in the dune areas, without eliminating the use of groundwater for the public water supply. Such attempts can only succeed when the whole hydrological system of the island is the subject of study and when a change in the techniques of drinking water production is considered. A working group consisting of hydrologists, ecologists, farmers, and administrators discussed the possibilities of 'integrated water resources management' (wise use of water) on the island (symposium of two days on the island). Several options were presented by this working group. Funds were assigned to this group to investigate the functioning of the hydrological regime and to assess the impact of hydrological changes on the ecological conditions in the dune-slack. After two years the results were available.

1991-1993: Scientific research on the functioning of the hydrological system

The hydrological research was carried out at the level of the whole island, but also on the detailed scale of an individual dune-slack. Hydrogeological research showed that dune-slacks affected by the abstraction of groundwater had relatively small catchment areas. Most of them were situated close to the centre of the island where the top of the freshwater body was situated. Geological research showed that thick clay layers were present in this area. However, these clay layers were not continuous, as the water company had always claimed, but there were wide sandy gullies within the clay layers, in which infiltration water could escape to the well field, instead of flowing to the dune slacks. Detailed hydrological and geochemical research was carried out in 1991 to evaluate future restoration prospects of the largest dune slack (‘Kapenglop’). About 250 water samples, obtained from mini-filters installed in deep borings (c. 24 m below soil surface) were analysed here for macro-ionic composition. Natural isotopes in the groundwater, such as ^{3}H, and ^{13}C, were measured for dating groundwater age. This was done to test reliability of the hydrological modelling. The exact location of the decalcification front was determined by $CaCO_3$ analysis in soil samples. The simulation of groundwater flow paths showed that the inflow of seepage water was only possible when the slack was flooded. Calcareous groundwater exfiltrated in the southern part of the slack, then proceeded as surface water and passed through the (anoxic) organic slack bottom in the central and northern infiltration parts. The CO_2 producing plant roots and the microbial population in the bottom sediments created a groundwater type that is highly reduced and aggressive towards calcareous substrates below the decalcification front. The distribution of ^{3}H and several dissolved ions was in accordance with the simulated groundwater flow pattern. These results were used to reconstruct the eco-hydrological conditions of 1950, a period with an abundance of typical dune-slack species, which had become endangered in later years. The simulation of groundwater flow fitted the form of the decalcification front underneath the slack remarkably well. The recent analyses of groundwater composition showed that the inflow of calcareous groundwater had decreased considerable and that infiltration characteristics prevailed. Underneath the slack high concentrations of very calcareous groundwater were found, indicating a rapid decalcification of the former seepage areas. The increased acidification had triggered a rapid accumulation of organic matter in the top soil, leading to a rapid decline of typical dune slack species, such as *Schoenus nigricans, Liparis loeselii, Epipactis palustris, Dactylorhiza incarnata* and *Pedicularis palustris,* in particular during wet summers, (Grootjans and others 1991). Although the impact of the groundwater abstraction was small (5-15 cm calculated water levels drawdown), which is close to the maximum accuracy of the hydrological model, the ecological consequences were very severe. Almost 99% of the former abundance of endangered dune slack plants was lost within 20 years.

The aforementioned hydrological system, therefore, is extremely sensitive to small changes in the hydrology. First of all the inflowing groundwater originates from very local recharge areas (100-200 m). Changes in the winter and spring water levels in these recharge areas are particularly harmful because they prevent calcareous groundwater from reaching the slack when it is flooded. The functioning of the slack as a flow-through lake appears to be the only mechanism to supply a slack surrounded by old decalcified dunes, with calcareous groundwater.

The research clearly showed that dune-slack species, such as *Liparis loeselli*, are growing in habitats that tolerate zero impact. Once the species have established, any decrease in groundwater input increased the speed of succession and thus the survival time of the population. Any increase in nutrient load favours competitive fast-growing shrubs and grasses and consequently also speeds-up successional processes.

1993-1995: Finding solutions

After a thorough study of the whole hydrological system the working group came up with several proposals: (1) conserve surface water in the polder area during wet periods; (2) store clean surface water from large drainage ditches in the polder area in a nearby freshwater pond that can act as a supply basin; (3) this clean surface water can be injected into deeper soil layers (deep infiltration) to be abstracted again when needed; (4) initiate a publicity campaign aimed at the tourists ('wise use of drinking water'); (5) disconnect the discharge of rain water into the sewage systems in urban areas; (6) initiate nature development (mainly sod cutting) outside the influence of the water production areas (compensation of damage to nature areas); (7) re-initiate sand blowing in suitable dune areas to promote the formation of new dune-slacks; and (8) transform part of the pine plantations into broad-leaved forest in the next decades. Ten years after the start of the project practically all suggestions were adopted by the authorities and most measures have been carried out already. The outcome of the project implies a further segregation of functions in the dune area (combination of urban functions with water production functions), but it stopped the gradual decline of nature conservation values in large parts of the dune area.

1996-2006: Monitoring restoration projects

Vegetation development and some soil parameters (accumulation of organic matter, pH, groundwater composition) are still being monitored in various restoration projects, outside the influence of the abstraction facilities. The measures consisted of large scale sod cutting in several slacks and cutting of planted alder wood in former dune-slacks. Due to these measures species such as *Liparis loeselii*, *Epipactis palustris*, *Schoenus nigricans* established new populations, although the original abundance of these species was never reached again.

This also shows that groundwater fed dune slacks in decalcified topsoils tolerate zero impact. Some regeneration after a change in hydrology is possible (Grootjans and others 2002), but a full restoration is not possible, at least not for a longer period of time (more than 10 years).

Research Information Note

English Nature Research Reports, No 696

Development of eco-hydrological guidelines for dune habitats – Phase 1

Report Authors: A.J. Davy, A.P. Grootjans, K. Hiscock and J. Petersen

Date: 2006
Keywords: dune slack, eco-hydrology, hydrological model, management, succession

Introduction

Many European Sites and Sites of Special Scientific Interest support habitat types which have some dependency on water resources, although our understanding of the specific eco-hydrological requirements of these habitats is often limited. A collaboration between English Nature, the Countryside Council for Wales and the Environment Agency is progressing a programme of work to further our understanding of the eco-hydrology of a range of such habitats. Work initially focussed on mire and wet grassland habitats and developed an approach to conceptualising water requirements termed the 'Wetland Framework'. Having recognised the value of this approach for other wet habitats, this report presents the results of a review of the eco-hydrological requirements of dune slack habitats, and where possible gives 'interim' advice for establishing eco-hydrological guidelines to assist casework.

What was done

English Nature commissioned a review and evaluation of information on the eco-hydrology of dune slack habitats in Britain in order to assess how far it is currently possible to identify their water supply mechanisms and preferred regimes for water and nutrients. There were three main elements of the work:

1 A review of published and unpublished eco-hydrological information on dune slack habitats and species.

2 A critical evaluation of the reviewed information.

3 Development of a preliminary conceptual framework for 'how dune slack habitats work' and interim recommendations for ecological target setting.

The report also considers the influences of climate, water supply mechanism, nutrient regime and management and draws heavily on work conducted in the Wadden Sea area of Europe.

Continued……

Results and conclusions

The first part of the report reviews current understanding of the interactions between vegetational succession, sand buffering capacity (calcium carbonate content) and hydrology. As there has been relatively little scientific work in Britain, the review draws heavily on extensive work carried out in the Wadden Sea area, along the coasts of The Netherlands, Germany and Denmark.

The second part of the report concentrates on critical evaluation and the identification of research needs. Information on the hydrological conditions in a range of European dune slack habitats is used to develop a new conceptual model for dune-slack hydrology, based on a water balance approach. The conceptual model can be used to assess the hydrological sensitivity and hydrochemical consequences of, for example, groundwater abstraction. Field measurements and quantitative modelling studies in Britain are required to validate this model and refine its predictive capability.

Extrapolating experience from the Netherlands suggests that dune slacks may be irreversibly sensitive to water abstraction, recharge variation and changes in water quality. Recommended interim targets would be for minimal impact until the small area of British dune slacks is much better understood.

English Nature's viewpoint

The review represents the first step in establishing robust eco-hydrological guidelines for dune slack habitats. Further work is needed to give confidence in the conceptual models suggested but in the short-term, the information presented will guide thinking about the eco-hydrological requirements of dune slack habitats, for the purposes of casework and the development of future research.

Selected references

GROOTJANS, A.P., and others. 2002. Restoration of coastal dune slacks in the Netherlands. *Hydrobiologia*, 478, 181-203.

JONES, P.S. 1993b. The importance of hydrological processes in sand dune ecosystems. *In:* ATKINSON, D. & HOUSTON, J. eds. *The dunes of the Sefton Coast*, 59-62. Liverpool: National Museum and Galleries on Merseyside.

PETERSEN, J. 2000. *Die Dünentalvegetation der Wattenmeer-Inseln in der südlichen Nordsee. Eine pflanzensociologische und ökologische Vergleichsuntersuchung unter Berücksichtigung von Nutzung and Naturschutz.* University of Hannover: PhD thesis

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