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Changes in vegetation and soil characteristics in coastal sand dunes along a gradient of atmospheric nitrogen deposition

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Abstract: **A field survey was conducted to detect signals of atmospheric nitrogen (N) in 11 dune systems along a nitrogen deposition gradient in the United Kingdom. In the mobile and semi-fixed dunes, above-ground biomass was positively related to N inputs. This increase was largely due to increased height and cover of *Ammophila arenaria*. In the long term, this increased biomass may lead to increased organic matter accumulation and consequently accelerated soil development.**

In the fixed dunes, above ground biomass also showed a positive relationship with N inputs as did soil C:N ratio while soil available N was negatively related to N inputs. Plant species richness was negatively related to N inputs. In the dune slacks, while soil and bulk vegetation parameters showed no relationship with N inputs, cover of *Carex arenaria* and *Hypochaeris radicata* increased. Site mean Ellenberg N numbers showed no relationship with N deposition either within habitats or across the whole dataset. Neither abundance-weighting nor inclusion of the Siebel numbers for bryophytes improved the relationship. The survey reveals that the relationships of soil and vegetation with atmospheric N deposition vary between sand dune habitats but, despite this variability, clear correlations with N inputs exist. While this survey can not

establish causality, on the basis of the relationships observed we suggest a critical load range of 10 – 20 kg N ha^{-1} yr^{-1} for coastal sand dunes in the UK.

Key-words: Critical loads, global change, ellenberg indicator values, eutrophication, C:N ratios.

Introduction

Over the last 30 to 40 years, many UK sand dunes have changed from being actively mobile systems to landscapes with fairly continuous vegetation cover and only minor areas of blowouts or shifting dunes (Hope-Simpson, 1997[15]; Rhind et al., 2001[32]). This relatively rapid stabilisation, the loss of early successional habitats and the observed increase at many sites of tall rank grassland and woody species is causing concern among conservation agencies. Atmospheric N deposition has approximately doubled in Europe over a similar timescale and is implicated in biological changes in other oligotrophic habitats such as Dutch heathlands (Heil and Diemont, 1983[12]; van der Eerden et al., 1991[39]) and the UK uplands (Haines-Young et al., 2000[11]). While the changes in dune vegetation may also be due to climatic influences, changes in management practices, and a general decline in natural and managed grazing (Dargie, 1995[7]; Radley, 1994[30]; Ranwell, 1960[31]), it was concern about the effects of atmospheric nitrogen which initiated this study. Early nutrient addition experiments (Pemadasa and Lovell, 1974[28]; Willis, 1963[42]; Willis, 1965[43]) were of short duration, using large dose, high concentration nutrient applications. While useful in highlighting which species may respond to N enrichment, they are of limited use in understanding the long term consequences of continuous, low concentration atmospheric inputs, although work in the Netherlands has begun to address these issues (ten Harkel et al., 1998[36]; ten Harkel and van der Meulen, 1996[37]).

There is therefore a need to assess the broad impacts of N deposition on dune habitats and this study utilised a field survey approach to take samples from sites representing a gradient of nitrogen deposition. The aims were to 1) Detect signals of atmospheric N inputs in the soil and vegetation; 2) Test the suitability of Ellenberg N index values for assessing nitrogen impacts in other dune systems in the UK and; 3) Suggest a critical load range for UK sand dunes.

Methods

Ten sites were initially chosen to encompass a gradient of N deposition and a range of geographical locations around England and Wales. Over the course of the field survey, one extra site, Great Yarmouth, was included to increase representation of the lichen rich dune grassland communities in Norfolk. One year later, soil samples were obtained from three relatively low N sites in the Outer Hebrides, Scotland for comparison. The sites are characterised in Table **1**.

Calculating Nitrogen Deposition

The N deposition data for each site (Table **1**) were calculated using wet deposition data for the UK for 1997, extrapolated from a network of monitoring sites (NEGTAP, 2001[25]); combined with dry deposition data based on diffusion tube measurements of NO_2 and NH_3 concentrations at each dune site for May and July, 2001 which were taken to represent an annual mean. This approach was validated by regression with tissue N content of the moss *Hypnum cupressiforme* and gave a strong correlation (R^2 = 36.6 %, p = 0.084). As NH_3 and NO_2 concentrations were not measured at Great Yarmouth, N deposition for this site was calculated by regression using tissue N content of moss samples. Full details of estimating the

N deposition for this study can be found in Jones et al. (2002[18]; 2002[19]). Nitrogen deposition for the Hebridean sites was calculated from NEGTAP (NEGTAP, 2001[25]). These sites were not used in the analysis and are included for comparison only.

Field Survey Methodology

The field survey was conducted in May 2002, although some additional soil samples collected from the Outer Hebrides in June 2003 are included in the results. Within each sand dune system, sampling of soil and vegetation was conducted along a transect inland from the coast, stratified to incorporate samples, where present, from the following habitat types: mobile dunes; semi-fixed dunes; fixed dunes and established dune grassland; and dune slacks. Eight survey points were sampled along each transect, although only four were conducted at Studland and Great Yarmouth, and seven conducted at Winterton and Seaton due to the homogeneity of the vegetation communities and the lack of dune slacks at these sites. At each survey point an area of homogenous vegetation was identified and two, 2 m x 2 m, quadrats established within an area of c. 20 m radius. Sward height at three random points was measured and percentage cover of all vascular plants, bryophytes and lichens within the quadrat was determined. On two corners of each quadrat, a 5 cm diameter, 15 cm depth soil core was removed for soil analysis, and a 25 x 25 cm area of vegetation clipped to ground level for above ground biomass and tissue N determination. This was increased to 50 x 50 cm in the mobile dunes to ensure a representative sampling area. All soil samples were stored in a 4 °C cold-room prior to laboratory analysis. At each site, a number of moss samples were taken for tissue N analysis. *Hypnum cupressiforme* was the only widespread moss species and was present at all sites except Seaton. Therefore, only this species was used for tissue N determinations.

Analysis of vegetation samples

Biomass samples were oven dried at 65 °C to constant weight before weighing. Sub-samples of total above-ground biomass were ground to 0.5 mm and analysed for %N content on a Leco 2000 CHN analyser. Further sub-samples from the fixed dune grasslands were analysed for nitrogen (%N) and phosphorus (%P) content by Kjeldahl acid digest followed by dilution and analysis by ion chromatography, in order to determine N:P ratios. N pool data are presented as kg N ha^{-1}. Samples of the moss *H. cupressiforme* were prepared by cleaning and separating the live portion of shoots (approximately 3 cm of shoot). The samples were then ground to a fine powder prior to analysis for %N content on a Leco 2000 CHN analyser.

Analysis of soil samples

The two replicate cores from each vegetation quadrat were bulked for chemical analysis. The soil horizons were not separated. Soil pH was measured in 0.01 M $CaCl_2$ solution (1:2.5 w.b.v). Soil moisture and Loss on Ignition (LOI) were determined by drying and re-weighing soil samples at oven temperatures of 105 °C and 375 °C for 12 hours, respectively (MAFF, 1986[23]), with the oven temperature for LOI reduced to 375 °C to minimise CO_2 losses from $CaCO_3$. Available NH_4 and NO_3 were determined by extraction with 1.0 M KCl. The filtrates were analysed using continuous segmented-flow colorimetry. Available PO_4 was determined by the Olsen - P method. The resulting filtrates were analysed on an auto analyser using the molybdate – blue method. The total N and total C contents of soil were determined on air dried soil using a Leco 2000 CHN analyser. However, total N contents in soils from the mobile and semi-fixed dunes were below detectable limits for this machine and N contents for these samples were determined by Kjeldahl acid digest followed by dilution and analysis using ion chromatography. In all analyses, Quality Assurance was conducted by inclusion of laboratory blanks, duplicates and standard soils. N pool data are expressed as kg N ha^{-1} for the top 15 cm soil layer. All other data are expressed as mg 100g dry $soil^{-1}$.

Statistical analysis

The vegetation quadrat data was analysed by detrended correspondence analysis (DCA) using CANOCO for Windows 4.5. The DCA revealed strong differences between the principal habitat types. Therefore for the majority of the analyses, the dataset of soil and vegetation parameters was subdivided into three main categories on the basis of the groupings observed. These were: 1) Mobile and semi-fixed dunes, 2) Fixed dunes and established dune grasslands and 3) Dune slacks. As the broad aim of this study was to assess surveyed parameters for effects of N deposition and as each site has only one deposition value, measured parameters of soil and vegetation were averaged to give a mean for each habitat at each site. The relationship between site parameters and N deposition was examined using linear regression. Each parameter was also checked for significant soil pH effects. Where significant relationships with pH occurred, pH was included as the first term of the regression to separate these effects from those of atmospheric N. Ellenberg numbers for vascular plant species were taken from Hill's modified Ellenberg numbers for the UK (Hill et al., 1999[14]) and an equivalent index from Siebel (1993[34]) was included for bryophyte species. Mean and abundance-weighted values per quadrat were calculated for vascular plants on their own and vascular plants plus bryophytes. The relationships between Ellenberg N and a number of soil parameters were assessed using linear regression. Ellenberg N was strongly related to soil pH (R^2 =19.9 %, $p < 0.001$). Therefore, soil pH was included as the first term of the regression in order to remove the effects of pH from the analysis. The mean Ellenberg N indicator for each site was also calculated and the relationship with N deposition assessed using linear regression as above. Unless otherwise stated, all statistical tests were carried out using Minitab 13.32.

Results

Mobile and semi-fixed dunes

There was a significant positive relationship of N inputs with above ground biomass (Table **2**, Fig. **1a**), and consequently with the vegetation N pool. Although not significant at the 95% level, sward height appeared to increase with N inputs to a maximum of roughly 80 cm (Fig. **1b**). There were no significant relationships between N inputs and any soil parameters. C:N ratios were not calculated for these habitats due to the very low levels of soil %N and soil %C. Mean Ellenberg N values in the mobile dunes were not related to N inputs. There was a trend of increased percentage cover of *Ammophila arenaria* in response to N inputs (Table **3**) although this was not significant at the 95% level. None of the other species showed a significant response.

Fixed dune grasslands

There was a significant positive relationship between N inputs and above ground biomass (Fig. **2a**) once the effects of pH had been removed, and a positive increase in the vegetation N pool, although this was not significant at the 95% level (Table **2**). There was also a significant negative relationship between N inputs and species richness (Fig. **2b**). N inputs were negatively related to soil available N (Fig. **2c**) and positively related to soil C:N ratio (Fig. **2d**). However, neither the total N in the soil nor the available N content of the organic matter showed any relationship to N inputs. Mean Ellenberg N values in the fixed dunes were not related to N inputs. *Carex arenaria* showed a significant positive response to N inputs and was the only species in this habitat to do so (Table **3**).

Dune slacks

There were no significant relationships of N inputs with any of the soil or vegetation parameters in the dune slacks (Table **2**). Mean Ellenberg N values in the dune slacks were not related to N inputs. However, percentage cover of both *C. arenaria* and *Hypochaeris radicata* showed a significant positive response to N inputs (Table **3**).

Ellenberg N Numbers and N:P ratios

Using regression to allow for the effects of pH, and including the full data set of all 156 quadrats and associated soil and vegetation samples, the mean Ellenberg N numbers were negatively related to soil available N per gram organic matter in the mobile dunes (R^2 = 20.2 %, p = 0.039), and positively related to soil %N (R^2 = 36.2 %, p = 0.016) and to soil organic matter (R^2 = 36.3 %, p = 0.022) in the fixed dunes. Ellenberg N numbers did not relate significantly to any of the soil and vegetation parameters in the dune slacks. Despite the significant relationships of atmospheric N deposition with various soil and vegetation parameters in the mobile and fixed dunes, the mean Ellenberg N number per site was not significantly related to atmospheric N deposition in any of the habitats, or across the data set as a whole. Neither abundance-weighting nor inclusion of the Siebel bryophyte numbers improved the relationship of mean Ellenberg N with atmospheric N deposition. N:P ratios of total above ground vegetation in the fixed dune grasslands ranged from 5.0 to 15.6 indicating borderline P limitation in some samples. However, ratios varied strongly both within sites and between sites. There was no significant relationship between soil available P and N:P ratios in the vegetation, and there was no relationship between site mean N:P ratios and N deposition.

Discussion

Mobile and semi-fixed dunes

Results suggest that there is a relationship between N deposition and biomass in the mobile dunes, largely accounted for by an increase in sward height and an increase in cover of the dominant species *A. arenaria*. Studies aimed at improving dune stabilisation showed that the classic European dune-binding species (*A. arenaria*, *Elytrigia juncea* and *Leymus arenarius*) all responded to fertiliser applications (Adriani and Terwindt, 1974[2]; Greipsson and Davy, 1997[10]), as did a study on *Ammophila breviligulata* in Canada (Boudreau and Houle, 2001[6]), although a Canadian study on foredune vegetation showed no increase in plant growth following N and P additions (Houle, 1997[16]). Pot studies have also shown that *A. arenaria* increases tillering and leaf length with increased nitrogen supply (Pavlik, 1983[27]). The long term implications of this increased biomass may therefore be to accelerate rates of organic matter accumulation and consequently soil development. This will lead to a reduction in the area of the mobile components of these dune systems, and more rapid stabilisation of an ecosystem whose long term existence is dependent on the dynamics of windblown sand. A further consequence of more rapid nitrogen accumulation in the soil may be to alter the course, or even the endpoint, of the usual dune succession.

Fixed dune grasslands

The negative relationship of N inputs with available N is surprising. A plausible hypothesis is that atmospheric deposition is reducing the activity of nitrogen fixing organisms and therefore nitrate production. Inputs from N-fixation by cyanobacteria on damp sand in dune grassland have been estimated at 25 kg N ha^{-1} yr^{-1} (Stewart, 1967[35]), although extrapolation of data from Johnson (Johnson, 1979[17]) suggests that inputs from legumes in dune grasslands may only be in the order of 5 kg N ha^{-1} yr^{-1}. Nevertheless, these amounts are equivalent to inputs from atmospheric deposition and represent a significant part of the N budget. An alternative hypothesis may be that the increased plant growth is leading to depletion of available N in the soil. The soil C:N ratios show a similar range to those reported by Kooijman and Besse (2002[22]), although the positive relationship with N inputs is again surprising. A similar increase in C:N ratios has been shown in some forest soils (Billett et al., 1990[5]). While these relationships appear counter-intuitive, they are reinforced by the soil data from relatively pristine air-quality sites in the Outer Hebrides. Berendse (1998[3]) suggests that during the course of succession, as more woody species appear, the litter contains more phenols and organic compounds and decomposition rates slow down. However, there was no obvious shift towards more woody species at the high N sites. Increased N deposition can also result in slower long-term litter decomposition in N-saturated forest systems as the C-supply becomes limiting for microbial degradation (Berg et al., 1998[4]). There is clearly further research needed to elucidate the mechanisms behind the observed relationship of N with C:N ratios.

Dune slacks

The lack of significant responses of biomass and soil parameters in the dune slacks is surprising, since Willis (1963[42]) showed that dune slack vegetation at Braunton Burrows responded to N applications. However, the increases in cover of *C. arenaria* and *H. radicata* show that individual species may be responding to increased N deposition, even if major vegetation changes are not evident across the N deposition gradient. This may, in part, be due to the absence of dune slacks at two of the high N sites.

Ellenberg Indicator Values and N:P ratios

Ellenberg N values in this study did not reveal changes in the vegetation in response to the N deposition gradient. As in other studies (Hill and Carey, 1997[13]; Melman et al., 1988[24]; Pitcairn et al., 2003[29]), neither abundance-weighting nor inclusion of the Siebel indicators for bryophytes improved the relationship with N deposition. Due to the variety of species and vegetation communities encountered across the survey, it was hoped that Ellenberg N values would be able to provide a unifying approach to analysing potential N responses. However, this approach was not successful. As identified by Hill & Carey (1997[13]) and Schaffers & Sykora (2000[33]), Ellenberg N seems to be a general indicator of soil fertility rather than specifically a nitrogen index. Secondly, in habitats such as the mobile dunes, the available species pool is restricted to those species capable of surviving the harsh physical conditions of water stress, salinity and disturbance, thus limiting potential changes to community composition in response to N inputs. Despite their usefulness in detecting change over time in other dune systems (van der Maarel et al., 1985[41]) and eutrophication effects in forests (Diekmann and Dupré, 1997[8]), they were of limited use in this study, and a recent UK study along a local gradient of NH_3 deposition (Pitcairn et al., 2003[29]) also showed no significant relationship with Ellenberg N values.

Phosphorus availability may limit community responses to N deposition and N:P ratios can be used to determine which element is more limiting to plant growth, with ratios above 16 indicating P limitation (Koerselman and Meuleman, 1996[21]). In this study the N:P ratios did not suggest greater P limitation with increasing N deposition, and observed vegetation responses were reasonably consistent across the N deposition gradient. The two sites with the highest N deposition had relatively high available P levels in the soil which may have contributed to these sites remaining N limited. Therefore it is unlikely that P limitation has dramatically influenced the observed relationships with N deposition.

The impacts of N deposition have been mentioned by several authors in relation to dunes in north west Europe (Dopheide and Verstraten, 1995[9]; Ketner-Oostra, 2001[20]; Ovesen, 2001[26]; van der Laan, 1985[40]) but these impacts have rarely been quantified, with the exception of Dopheide and Verstraten (1995). This is therefore the first published systematic survey which identifies relationships between N inputs and the soil and vegetation of dune systems.

Critical Loads

This survey has shown relationships of a number of parameters with N inputs which include: Increased biomass in the mobile and fixed dunes; Increased cover of certain species in the fixed dunes and dune slacks; Reduced N availability and increasing C:N ratio in the fixed dunes. While this survey only shows an association and not causality, on the basis of these results it appears likely that the sites with higher N deposition are exceeding the critical load for nutrient nitrogen for sand dunes. In many of the variables where significant relationships with N inputs were observed, a threshold at around 15 kg N ha^{-1} yr^{-1} seemed to differentiate between the response of the cluster of sites experiencing low N inputs and the responses of those sites experiencing higher loads of N deposition. This reinforces findings by Dutch authors using a mesocosm approach (Tomassen et al., 1999[38]). Therefore, acknowledging the precautionary principle behind the critical load concept, and the need to account for different base status and degree of management at sites (Achermann and Bobbink, 2003[1]), a preliminary critical load range of 10 – 20 kg N ha^{-1} yr^{-1} is proposed for mobile and fixed sand dune systems. There are not enough data to suggest a critical load for humid dune slacks.

This suggested critical load is an important first step towards providing protection of a valuable European habitat which, until now, has not been included in the critical loads manual (Achermann and Bobbink, 2003[1]). However, further studies are necessary to validate the suggested critical loads for dry dune habitats and, in particular, to examine potential effects of N in dune slacks.

In conclusion, the results of this field survey suggest that atmospheric N deposition is having an effect on soil and vegetation in some sand dune sites in England and Wales. However, there does not appear to be one single indicator of excess N deposition which is common to all sites, and different variables respond in different dune habitats. Integrated indices such as Ellenberg N values have not proved to be of use in this survey. There is considerable work required to improve our understanding of the long term consequences of enhanced N deposition in the dry dunes and in dune slacks. There is also a need to build on the results of this survey to develop reliable indicators of excess N deposition in dune systems.

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Table 1 Characterisation of the eleven sand dune sites surveyed in England and Wales, and three sites from the Outer Hebrides, Scotland included for comparison. * Nitrogen deposition value for Great Yarmouth estimated using regression relationship of moss tissue N against calculated N inputs established from the other sites. † Nitrogen deposition estimated from NEGTAP (2001).

Site name	Number of sample points	Approximate latitude and longitude		pH range	Range of available soil phosphorus (mg 100g dry soil^{-1})	Calculated nitrogen deposition (kg N ha^{-1} yr^{-1})
Wales						
Newborough Warren, Ynys Mon	8	53:08N	4:21W	4.5 - 7.2	0.033 – 0.234	12.35
Morfa Harlech, Meirionedd	8	52:52N	4:08W	4.9 - 7.1	0.062 – 0.088	12.22
Pembrey Coast, Carmarthenshire	8	51:40N	4:17W	5.7 - 6.9	0.034 – 0.065	10.31
Kenfig Burrows, Glamorgan	8	51:31N	3:44W	5.7 - 6.7	0.063 – 0.088	11.02
Merthyr Mawr, Glamorgan	8	51:29N	3:38W	5.8 - 6.7	0.066 – 0.092	15.38
England						
Ainsdale, Lancashire	8	53:35N	3:04W	4.5 - 6.6	0.042 – 0.422	12.86
Studland, Dorset	4	50:40N	1:57W	3.1 - 6.0	0.042 – 0.359	15.63
Great Yarmouth, Norfolk	4	52:38N	1:45E	3.8 - 6.6	Not measured	19.49*
Winterton, Norfolk	7	52:43N	1:42E	3.3 - 6.5	0.068 – 0.379	29.4
Seaton, County Durham	7	54:39N	1:10W	5.7 - 6.7	0.271 – 0.345	25.22
Bamburgh, Northumberland	8	55:36N	1:42W	5.5 - 6.7	0.080 – 0.117	19.33
Scotland (Hebrides)						
Baleshare, North Uist	3	57:31N	7:27W	6.3 - 6.8	Not measured	9.8†
Borve, Benbecula	3	57:26N	7:24W	6.4 - 7.1	Not measured	8.5†
Tobha Mor, South Uist	3	57:17N	7:22W	6.5 - 7.0	Not measured	6.9†

Table 2 Site mean values for soil and vegetation parameters measured during the survey, split by habitat type. Data in each cell show the mean across all sites (top line) and the variation between site means (minimum and maximum values – bottom line). Parameters showing a significant regression relationship with nitrogen inputs are shown in bold. The sign (+/-) indicates the slope of the relationship. (+/-) P < 0.1; +/- P < 0.05; ++/-- P < 0.01; +++/--- P < 0.001. Those with a hash (#) represent variables where the effect of soil pH was significant and pH was included as the first term in the regression in order to remove its effect from that of the nitrogen gradient.

	Mobile and semi-fixed dunes	Fixed dunes and dune grasslands	Dune slacks
Vegetation			
Biomass	**1349 +**	**# 1164 +**	# 1274
($g\ m^{-2}$)	**(571 - 2463)**	**(408 - 1956)**	(664 - 1848)
Sward height	**57.5 (+)**	22.0	27.5
(cm)	**(27.5 - 89.2)**	(2.0 -43.4)	(16.2 - 41.5)
Tissue N content	0.84	1.21	1.19
(%)	(0.62 - 1.01)	(1.03 - 1.49)	(0.94 - 1.67)
Vegetation N pool	**111 ++**	**# 132 (+)**	148
($kg\ N\ ha^{-1}$)	**(58 - 200)**	**(49 - 202)**	(76 - 223)
Species richness	14.3	**21.0 -**	18.8
	(9.0 - 20.5)	**(13.1 - 28.8)**	(12.8 - 28.5)
Ellenberg N	3.9	3.7	3.8
	(3.1 - 4.3)	(2.5 - 4.4)	(3.6 - 4.1)
Soil			
Available N	0.24	**0.65 -**	0.47
(mg 100g dry $soil^{-1}$)	(0.12 - 0.43)	**(0.21 - 1.13)**	(0.16 - 0.79)
Available N	59.0	22.9	12.4
(mg 100g organic $matter^{-1}$)	(33.2 - 92.7)	(11.2 - 38.9)	(2.9 - 26.0)
Soil total N	0.032	0.099	0.216
(%)	(0.007 - 0.070)	(0.034 - 0.158)	(0.088 - 0.385)
Soil N pool	674	1604	2578
($kg\ N\ ha^{-1}$)	(146 - 1251)	(722 - 2553)	(1337 - 4365)
soil organic matter (OM)	0.64	3.34	5.13
(% Loss on ignition)	(0.22 - 1.47)	(1.20 - 7.89)	(2.74 - 10.24)
Soil C:N ratio	Not analysed	**22.1 +**	23.1
		(14.4 - 37.7)	(18.4 - 28.4)

Table 3 Site mean values of percentage cover of the four most common species, split by habitat type. For description of layout, refer to legend in **Table 2**.

	Mobile and semi-fixed dunes	Fixed dunes and dune grasslands	Dune slacks
Ammophila arenaria	**42.4 (+)**	8.8	Not analysed
	(31.3 - 55.5)	(0 - 30.1)	
Carex arenaria	2.7	**# 4.8 +**	**2.3 +**
	(0 - 8.8)	**(0.3 - 25.4)**	**(0 - 7.3)**
Festuca rubra	14.5	# 17.9	4.4
	(5.3 - 26.7)	(0 - 41.7)	(0 - 14.0)
Hypochaeris radicata	# 3.2	# 4.7	**0.3 ++**
	(0.3 - 9.3)	(0.3 - 17.5)	**(0 - 1.0)**

Fig. 1 Data from the mobile and semi-fixed dunes in relation to N inputs showing a) Above ground biomass (gm^{-2}) and b) Sward height (cm). Filled diamonds represent calcareous sites, open squares represent acidic sites. Bars show ±1 s.e.

a) **b)**

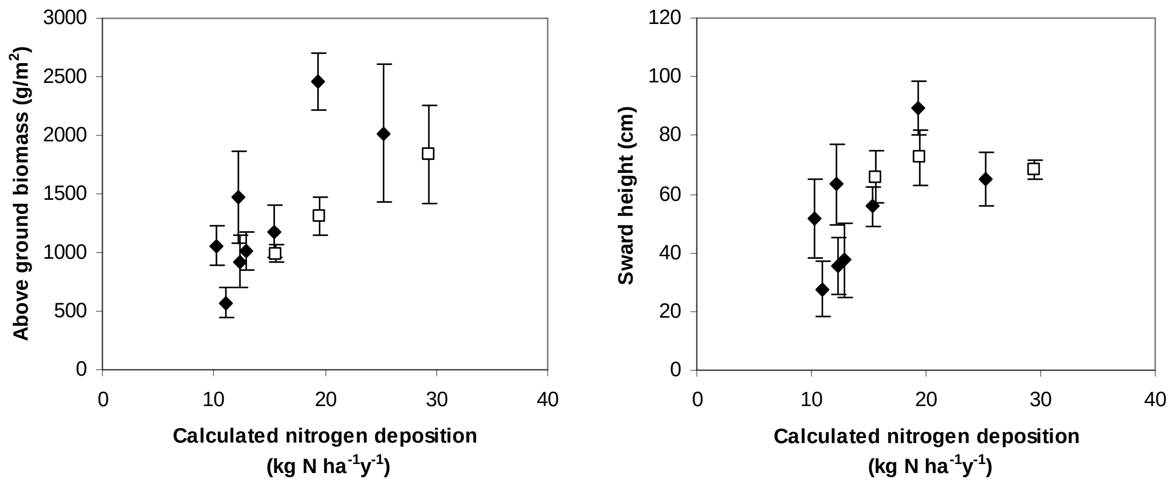

Fig. 2 Data from the fixed dunes and dune grasslands in relation to N inputs showing a) Above ground biomass (gm^{-2}), b) Species richness, c) Soil available N (mg / 100g dry $soil^{-1}$) and d) Soil C:N ratio. Filled diamonds represent calcareous sites, open squares represent acidic sites, triangles show soils from the Outer Hebrides for comparison (not included in the analysis). Bars show ±1 s.e.