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Eco-hydrological requirements of dune slack vegetation and the implications of climate change.

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Abstract

Dune slacks are a seasonal coastal wetland habitat, whose plant assemblages and soil properties are strongly linked to a fluctuating water table. Climate change is predicted to cause major shifts in sand dune hydrological regimes, yet we know remarkably little about the tolerance of these communities to change, and their precise hydrological requirements are poorly quantified. Dune slack vegetation and soils were sampled within five vegetation types across four west coast UK sites. Relationships between vegetation assemblages, and parameters of soil development (moisture, loss on ignition, pH, KCl extractable ions) and groundwater hydrological regime (annual maximum, minimum water levels and range, duration of flooding) were established to define the environmental tolerances of different communities. In multivariate analysis of the vegetation, the dominant gradient was hydrological: dry to wet, followed by a secondary soil development gradient: young calcareous organic-poor soils to acidic/neutral soils with greater organic matter contents. Most measured hydrological and soil variables explained a significant proportion of observed variation in species composition when tested individually, with the exception of soil nitrate and soil calcium concentrations. Maximum water level was the key hydrological variable, and soil moisture and soil pH were the key soil variables. All hydrological and soil parameters together explained 22.5% of the total species variation. There were significant differences in hydrological and soil parameters between community types, with only 40 cm difference in mean annual minimum water levels (averaged over four years) separating the wettest and the driest dune slack communities. Therefore, predicted declines in water level exceeding 100 cm by 2080 are likely to have a major impact on the vegetation of these priority conservation habitats.

Keywords: hydroecology; sand dunes; groundwater; global change; water table.

1. Introduction:

Sand dunes are rich in biodiversity due to the heterogeneity of habitat niches, and have both considerable amenity value and a strategic function as coastal defence (e.g. Everard et al. 2010; Louisse and van der Meulen, 1991). Dune slacks are seasonally flooded humid depressions between dune ridges, and are a priority habitat for rare species of conservation importance, including orchids such as Liparis loeselii, Dactylorhiza praetermissa and Dactylorhiza purpurella, lower plants like Petalophyllum ralfsii, a liverwort listed in Annex II of the European Union Habitats Directive, and amphibians like Epidalea calamita which breed in temporary pools (Smith, 2006). Many of these species are restricted to pioneer or successionally young vegetation communities (Davy et al., 2006; Rhind and Jones, 1999; Sival et al., 1998) where competition is low.

Dune slacks form when bare sand is disconnected from seawater influence by the establishment of a new dune front, or inland, where wind erosion scours bare sand down to the water table or to the capillary wetted layer (Ranwell, 1960). Thus their formation and subsequent plant and soil development are intimately connected to the dune groundwater hydrological regimes. Large water table fluctuations are a feature of most slacks, and control slack vegetation development. Variation of water levels occurs both within the year, typically around 70 cm with a rapid rise in autumn and a gradual decrease from spring to summer (Ranwell, 1959) and between years, depending on precipitation and evapotranspiration balances (Ranwell, 1959).

Winter flooding, intensity of drought and persistence of waterlogging in the rooting zone during the growing season are key environmental factors affecting vegetation, through impacts on germination and productivity (Ernst, 1990; Grootjans et al., 1998). The timing and duration of these events can alter inter/intraspecific competition, thus changing community composition (Bossuyt et al., 2003; Bossuyt et al., 2005). Groundwater fluctuations also control nutrient status: high water levels in slacks reduce the mineralisation of organic matter, maintaining low nitrogen and phosphorous levels (Lammerts and Grootjans, 1997). The chemistry of groundwater is important, and can vary considerably across a site (Jones et al., 2006). In older de-calcified dune slacks, buffering action of carbonate-rich groundwater allows the survival of basiphilous wetland plants (Grootjans et al. 1988, 1991; Sival et al. 1998; Van Dijk and Grootjans, 1993).

Most authors agree that species distribution and community structure across slacks are highly correlated with groundwater levels (Grootjans et al., 1991, 1998; Jones and Etherington 1971; Lammerts et al. 1998, 2001; Noest, 1994; Olff et al. 1993; Ranwell, 1960; Sival et al., 1998; Van der Laan 1979; Willis, 1959b). The differentiation as wet or dry slacks and the hydrological characteristics of different communities are well understood by ecologists (e.g. Rodwell, 2000). Yet, despite this, the precise eco-hydrological requirements of these communities are poorly, if at all, quantified in the UK. In the Netherlands there is a wealth of ecohydrological knowledge on dune slacks (e.g. Witte et al. 2007; von Asmuth et al. 2012), but slacks in the UK differ somewhat from those on the continent. In general they experience higher rainfall, they are often present on narrower dune sites with greater potential for groundwater influence from inland. In the majority of west coast sites, the sand parent material is usually more calcareous, resulting in highly buffered systems with slower decalcification rates, despite the higher rainfall. However, in north UK, slacks can be less well buffered and higher rainfall leads to decalcification of surface soils and rapid organic matter accumulation.

Previous attempts to define eco-hydrological requirements for UK dune slack communities have been based on relatively small numbers of combined vegetation and hydrology records (Ranwell 1959), and conducted at single sites (Jones, 1993; Ranwell, 1959). A further failing is the short duration of hydrological records considered: two years or less, with little understanding of longer term hydrological variability and whether the vegetation is in equilibrium with hydrological conditions (Davy et al., 2010).

Dune slack habitats worldwide are under increasing anthropic pressure from water abstraction, afforestation, urbanisation (Grootjans et al. 1998; Martinez et al., 2004; Provoost et al., 2011), nitrogen deposition (Jones et al., 2004; Plassmann et al., 2008; Sival and Strijkstra-Kalk, 1999) and from grass and scrub encroachment or exotic species invasion (Martinez et al., 2004). In addition, changes in evapotranspiration due to vegetation change or management will affect the water balance (Davy et al. 2010; Ford et al. 2012). An emerging threat is climate change, which may shift the biogeographical range of dune slack species, but which also alters the dune environment. Changes in precipitation and temperature affect groundwater levels directly by altering the delicate balance between rainfall and evapotranspiration, which controls recharge. Sea-level rise or shoreline erosion act indirectly on groundwater levels by altering water table gradients (Clarke and Sanitwong Na Ayutthaya, 2010; Saye and Pye, 2007). Modelling of groundwater trends for dune slacks in a sand dune system in north west England based on long term records, predicted a substantial lowering of water levels of 1 to 3 metres over the next 90 years (Clarke and Sanitwong Na Ayutthaya, 2010). Physiological adaptations typical of plants growing on humid calcareous substrates can make them less resilient to rapid habitat changes (Bakker et al., 2007; Grootjans et al., 2004; Schat, 1984) and the rapidity of community shifts in response to variations of groundwater regime is difficult to estimate (Noest, 1994; Van der Laan, 1979). The predicted changes in water levels are so large that major changes in slack vegetation are probable, but the outcomes will remain uncertain until we better understand the hydrological requirements of these vegetation communities.

The aim of this investigation was therefore to improve our understanding of the relationships between dune slack vegetation communities and the underlying hydrological and biogeochemical controls, across a range of west coast UK sites, through the following steps:

1. Creating a network of co-located vegetation and hydrological monitoring locations, maximising the use of previously unconnected long-term vegetation or hydrological data records.
2. Using multivariate analysis to determine the principle environmental parameters governing species assemblages in sampled dune slack communities.
3. Using hydrological data from a reasonably climatically stable four year period, to characterise the hydrological and environmental requirements of each community type.
4. Interpreting those requirements in the light of predicted climate change impacts on dune groundwater regimes.

Using this information, the following specific questions were postulated. Can vegetation communities be distinguished according to hydrological regime? Are projected changes in groundwater regime likely to have serious consequences for current dune slack assemblages?

2. Methods:

2.1 *Study sites*

Data were collected from four dune systems on the west coast of the UK (Table 1). Newborough Warren, a dune system located on the SW corner of the Isle of Anglesey in North Wales, UK, which contains all five of the UK slack communities. The sand dune area has developed between two estuaries; the western part of the dunes has been forested with Pinus nigra ssp. laricio commencing in 1948. Aberffraw, close to Newborough (~6km north west), is a smaller system about 1 km wide and extending 3 km inland, enclosed within a valley. Ainsdale Sand Dunes National Nature Reserve in the Sefton coast (Merseyside, UK), the largest area of open dune landscape in England, where part of the dunes are also forested (Pinus nigra ssp. laricio), and Whiteford Burrows National Nature Reserve, a spit dune system on the south side of the Loughor estuary, Gower Peninsula, South Wales. Here the dunes are bounded by saltmarsh on the east side and also partially afforested in the southeast. All sites are grazed by rabbits and, within fenced areas, are grazed by domestic livestock (Welsh mountain ponies, cattle and sheep). Climate in these locations can be defined as oceanic, with mild winters and cool summers. Long-term annual rainfall (1971-2001) at the sites varies from 828 to 1107 mm (Table 1); evapotranspiration in these dune slacks can vary between 360 and 550 mm/year depending on slack wetness and grazing pressure (Stratford et al., 2007).

[Table 1 about here]

2.2 *Vegetation communities*

In the UK, five dune slack vegetation communities have been described (Rodwell, 2000) with a number of sub communities. These vary from younger base-rich slacks through to older, decalcified communities, and range from wet to dry types. The main communities and subcommunities described in this study are summarised in Table 2, together with a dry dune grassland community (SD8), which forms the common dry end-point of the driest slack community SD16.

2.3 *Hydrological data.*

Even though water table levels and vegetation are monitored in several dune systems in the UK, their sampling locations rarely coincide. At Newborough there was an existing network of piezometers in the dunes, with the oldest hydrological records dating to 1985. The majority of wells were located in a single community type, SD14, therefore new piezometers were installed in early 2010 in other vegetation types, and adjacent to permanent vegetation quadrats established in 1987 (Plassmann et al. 2010). Additional transects of wells were installed across natural vegetation gradients in three slacks. New piezometers were also installed at Aberffraw, while existing piezometers were used at Ainsdale and Whiteford Burrows (Table 1), giving a total of 58 useable piezometers across all sites.

Monthly manual measurements of groundwater levels were made in all 58 piezometers from early 2010 for a period of 18 months. Older data at monthly resolution were available since 2006 for 16 piezometers at Newborough. Automatic logging water level recorders (DIVER®, Schlumberger, The Netherlands) were located in some of these older piezometers, and additional loggers installed in a selection of new piezometers, providing higher temporal resolution and independent verification of water levels at these locations. However, for statistical analysis, monthly resolution manual data were used from all piezometers to maximise spatial coverage across the sites. A hydrological year commencing on 1st June, during the summer water table decline was used as the basis for summary variables, in order to reliably record minimum and maximum water table heights in the same year, since timing of the rapid autumn re-wetting can vary considerably from year to year. The following hydrological variables were extracted from monthly records for 2010 and for longer time series where available: minimum water level, maximum water level, 10th and 90th percentiles (in case of truncation of records), annual range (maximum minus minimum water level), an estimated duration of flooding (assuming that where the water table was at or above the ground surface flooding occurred for four weeks), annual median (only calculated from 2006 to 2009), seasonal (spring, summer, autumn, winter) averages and averages for spring months (March, April, May and June).

[Table 2 about here]

2.4 *Vegetation survey*

Vegetation was surveyed in 1 m x 1 m quadrats around existing and newly established piezometers. Quadrats were arranged as a cross around the piezometers, with an additional quadrat placed in the most homogeneous part of the stand. Species occurrence was recorded as cover values (using visual estimates of percentage cover); nomenclature follows Clapham (1987) for vascular plants, since it is compatible with NVC community descriptions, and Hill (1991–94) for bryophytes. Physiognomical parameters, such as vegetation height, bare ground and litter cover, evidence of grazing, slope and aspect, were recorded for each quadrat. The location of the centre of each quadrat was recorded using a Leica 1200 RTKGPS.

2.5 *Topographical resolution*

Elevation of the ground surface at each piezometer and each quadrat was also measured using the Leica 1200 RTKGPS, with a vertical accuracy of ±1 cm. This provided elevation relative to the water table measured at nearby piezometers, used to derive adjusted hydrological summary data for each quadrat. Field-testing showed that water table height varied by less than 5 cm within 7 m of a piezometer and this was deemed acceptable variation without adjustment. At greater distances groundwater depth was measured using an auger, or quadrats were excluded from analysis.

2.6 *Soil survey and laboratory measurements*

At each quadrat a soil sample was collected, 5 cm in diameter to a depth of 15 cm. Samples were stored in the dark at 5º C until processed. After measuring depth of the organic horizon, large roots were removed and the samples thoroughly mixed. Ten grams of mixed fresh sample were weighed and dried overnight at 105° C to measure moisture content. Loss On Ignition was calculated by re-weighing the samples after 16 hours at 375° C. pH was measured after 30 min equilibration of 10 grams dry soil stirred in 25 ml deionised water, with pH electrode calibrated with standard solutions. Water-extractable soil nutrients were sampled using a solution prepared with 5 grams of dry soil in 45 ml of ultra high purity water (1:10 wt/vol), shaken for 24 hrs at 70 rpm in the dark followed by centrifugation at 5000 rpm for 10 minutes, and finally filtered through 0.45 μm cellulose nitrate filters. Extracts were analysed using a Metrohm ion chromatograph. Reference soils and duplicates were used for quality assurance.

2.7 Statistical analysis

Groups of quadrats with similar vegetation were identified using cluster analysis in TWINSPAN (Two-Way INdicator SPecies ANalysis, Hill, 1979b). The UK National Vegetation Classification (NVC) unit (Rodwell, 2000) for each of these clusters was assigned using MATCH software (Malloch, 1998). In order to determine whether quadrats represented ‘core’ good quality vegetation or ‘transitional’ vegetation, they were also assigned individually to an NVC unit using MATCH. If the quadrat assignation matched that of its parent cluster, it was classed as ‘core’, if it did not match, or was intermediate between two or more communities it was classed as ‘transitional’. Mean unweighted Ellenberg scores for light (L), moisture (F), reaction/pH (R) and nutrients (N) (Ellenberg et al., 1991) were calculated for each quadrat using UK Ellenberg indicator values for vascular plants and bryophytes (Hill et al., 1999).

The relationship between the vegetation and environmental variables was explored through indirect gradient methods using Principal Component Analysis (PCA) after testing the length of the first gradient for linearity of response gradients (CANOCO 4.0, ter Braak and Smilauer, 1998). The main hydrological and soil parameters were then used in a direct gradient method using Canonical Correspondence Analysis (CCA) for a subset of 189 quadrats, excluding those too far from the piezometers or with missing data. Significance of environmental variables in the CCA was assessed using Monte Carlo methods within CANOCO.

Since the majority of piezometers had only one year of hydrological records, it was explored whether piezometers with longer time series could be used to extrapolate longer-term hydrological trends. Average annual values for the hydrological parameters minimum water level, maximum water level and range were calculated for a four year sequence (2006 – 2009) for twelve piezometers located in the main dune slack community types. Relationships between the longer-term data and the data for 2010 were established using linear regression, and were all significant (Maximum water level, $R^2 = 89.2\%$, $p < 0.001$; Minimun water level, $R^2 = 96.6\%$, $p < 0.001$; Range, $R^2 = 37.4\%$, $p = 0.009$). These equations were used to calculate four-year averages for the wider set of piezometers and associated quadrats. Frequency distributions of water levels for each community were calculated from mean and standard deviation of annual median water levels calculated for all quadrats within each vegetation community type, assuming a normal distribution.

Differences between vegetation clusters (or NVC units) for the main hydrological (minimum and maximum water levels, and annual range) and other environmental variables (soil pH, soil moisture and percentage Loss On Ignition, percentage bare ground and litter) were assessed by Analysis Of Variance, performed on the 2010 variables using Minitab v. 16. Summary hydrological data for each community were calculated from the four-year averages predicted from regression analysis. Data transformation was necessary for almost all soil elements, since data were not normally distributed (Kolmogorov-Smirnov test). Chloride, phosphate, sulphate, nitrate, potassium and sodium were natural log transformed, ammonium was square root transformed. Nitrite was excluded from the analysis due to excessive missing values.

3. Results:

The initial cluster analysis allocated the 245 quadrats to seven dune slack and grassland units of the UK National Vegetation Classification (Rodwell, 2000). To illustrate differences in the hydrological regimes underlying the main communities, Figure 1 shows typical hydrographs over four years from piezometers located in each of the main community types at Newborough Warren. The Potentilla anserina-Carex nigra (SD17) and Salix repens-Calliergon cuspidatum (SD15) communities experienced higher winter water tables and more frequent surface flooding of 10/20 cm compared to the other units. The Salix repens-Campylium stellatum community (SD14, only Bryum pseudotriquetrum-Aneura pinguis SD14c subcommunity shown) showed less annual fluctuation with lower winter but higher summer water table levels. The driest slack community Salix repens-Holcus lanatus (SD16) had generally lower water tables throughout the year. The groundwater levels underlying dry dune grassland Festuca rubra-Galium verum (SD8) were considerably lower throughout and are shown for comparison.

[Figure 1 about here]

The PCA shows the pattern of variation in the quadrats, coded according to vegetation community (Figure 2), with environmental variables (bottom right) overlain for interpretation. The primary axis of variation corresponds to a wetness gradient: Ellenberg F, all the hydrological variables and to a lesser degree soil moisture, were positively correlated with axis 1 scores. The second axis corresponds to soil development, with Ellenberg N, %LOI and NH_4^+ positively correlated whilst Ellenberg L and R and soil pH were negatively correlated with axis 2 scores. The vegetation communities are arranged along these gradients as follows. The wettest units are SD15b and SD14b, the former extending to older (higher organic matter) and wetter soil conditions, the latter having lower organic matter concentration indicative of younger sites. Quadrats clustering as SD14c have high scores for Ellenberg L and R reflecting a species composition characteristic of an open, early successional habitat with abundant heliophilous and basiphilous species growing on young calcareous soils with a thinly developed organic layer. The dry slack community SD16 is concentrated at the right hand side of the diagram indicative of low soil moisture whilst variability along the second axis indicates that it can develop on substrates of varying ages. The dry dune grassland SD8 quadrats are next to those of SD16, associated with older and usually drier soils, although the two communities clearly have overlapping hydrological tolerances on this part of the hydrological gradient. SD14d occupies a position intermediate between the wet SD15b and dry SD16. SD17 is not as well defined as the other communities;

with only seven quadrats, however, it appears to occupy damper and more mature systems associated with SD14d and SD15b.

[Figure 2 about here]

[Figure 3 about here]

The CCA (Figure 3) shows the influence of the measured environmental variables (Figure 3a) on the position of all vegetation quadrats (Figure 3b) and of groups consisting only of core vegetation (Figure 3c). The dominant axis relates to hydrology and the second axis to soil development, as in the unconstrained gradient analysis (Figure 2). Communities occupy broadly the same niches as seen in PCA, with some distinctions. The SD8 dry dune grassland and the wet slack SD16 are more clearly separated along the wetness gradient, and communities are more clearly distinguished along the soil development (secondary) axis. However, a key component of Figures 3b and 3c is the very high degree of overlap of the communities along the hydrological gradient represented by Axis 1.

Significance testing using Monte Carlo permutation showed that the model with all variables was highly significant ($p<0.001$). The first four axes explained 61.6 % of the species-environment relationships, but explained a smaller proportion of the total species variance (first four axes 22.5%). Most variables tested singly were highly significant (Table 3), with annual maximum water level (6.3%) and soil moisture (6.3.%) explaining the greatest proportion of the total species variance. Only soil available nitrate and calcium were not significant explanatory variables. However, there was a high degree of correlation amongst the hydrological variables and all hydrological variables together explained only 8.9%. Hydrological and soil variables were largely orthogonal, with annual maximum water level, soil moisture and soil pH explaining 12.9% of species variance. An extended model combining key hydrological (maximum water level), soil (%moisture, soil pH) and soil chemistry parameters (NH_4^+, PO_4^-) increased the cumulative species variance to 14.6%. Ellenberg indicator values were separately tested as explanatory variables. Ellenberg F explained 10%, Ellenberg N an additional 7%, and a further 3% for Ellenberg R; when Ellenberg L was included in a combined model, together they explained 21.2% of the variance, similar to the proportion explained by the measured environmental variables.

Water extractable nutrients, presented as average ion concentration in six vegetation communities (combined data from core and transitional vegetation quadrats), showed significant differences between communities (Figure 4): calcium p=0.05, potassium p=0.01, all other ions p<0.001. Sulphate and phosphate had higher concentrations in SD17 as did nitrate. The other ions presented higher values in SD15b, except calcium, which was more concentrated in SD14 subcommunities. The SD14 subcommunities all had lower concentrations of nitrate, magnesium and potassium than the other communities.

[Figure 4 about here]

[Table 4 about here]

Hydrological parameters, the principal soil parameters and vegetation physiognomy were summarised for the main vegetation communities (Table 4). Minimum and maximum water levels differ significantly between the wetter slack communities (SD15b, SD14b), and the drier communities (SD16, SD14d). Winter water levels of the two wettest units (SD15b and SD14b) differ by around 20 cm from the slightly drier SD14c and SD14d whilst their summer minimum is at least 10 cm higher. The dry slack community (SD16) has mean winter and summer levels around 20-25 cm lower than the other slack types. The younger SD14c subcommunity appears to be intermediate in character regarding water levels, but its annual range (49 cm) is much lower than the others (~70 cm). Winter water tables in the dry dune grasslands (SD8) are a further 25 cm lower on average, although the wettest examples in this study have a winter maximum which overlaps much of the hydrological range of the dry slack community SD16 (Figure 5). %LOI and pH reflect soil age, with the youngest (SD14c) and older/wetter (SD15) communities differentiated, with the rest intermediate. The older, slightly decalcified, SD17 community, although poorly represented in this study, was not significantly different from SD15 in terms of hydrological and soil parameters, but diverged in bare ground and litter, with >25% plant litter compared with <4% in the other communities. Figure 5 shows the 67 and 90 percentile ranges for maximum winter water levels and minimum summer water levels for quadrats with core vegetation assemblages only. This shows clearly that the majority of core quadrats in the three main slack assemblages in this study have hydrologically distinct summer and winter water levels.

[Figure 5 about here]

4. Discussion:

This study has shown that dune slack vegetation assemblages are associated with distinct hydrological regimes, and with differing soil physical and chemical properties, in broad agreement with studies in the Netherlands (e.g. Lammerts et al. 2001). The cluster analysis and PCA axis scores demonstrated a clear separation of vegetation communities based on their species composition with Ellenberg F scores suggesting axis 1 was strongly linked to soil moisture. The majority of environmental variables tested through direct gradient methods (CCA) were significant in explaining species variation. However, although the proportion explained by the species-environment relationships is similar to published studies, e.g. 58 %

for the first two axes in Lammerts et al. (2001), surprisingly little of the overall species variation was explained by the measured environmental parameters. There are a number of potential reasons for this. Firstly, vegetation assemblages are the result of many factors, not just hydrological regime and soil development (Bakker et al., 2006). Inter-specific competition, migration rates and chance colonisation (Bossuyt et al., 2003; Bossuyt et al., 2005) introduce a high degree of heterogeneity to slack vegetation, even to adjoining slacks with similar hydrological regimes on the same site. A similar effect of site overriding hydrological parameters has been shown on floodplain meadows (Kalusova et al., 2009). Other factors such as secondary disturbance, and seed bank longevity also influence composition (Studer-Ehrensberger et al., 1993) and increase heterogeneity. Lastly, grazing pressure varies within and between sites and this may be a factor. However, Plassmann et al. (2010) showed that introduction of grazing had no major effect on slack vegetation at Newborough, with grazing effects secondary to both moisture and soil parameters. In these relatively young (20 – 150 years) well-buffered slacks prior to decalcification, although organic matter accumulates rapidly with age (Jones et al., 2008), slack age is a poor determinant of community type (Jones et al., 2010), nonetheless, it may be an important factor influencing vegetation composition. In contrast to some Dutch systems, salt spray, seawater influence and decalcification (Lammerts and Grootjans, 1998) are not dominant influences here; soil pH drops to a mean of 6.3 in the older SD17 community. Lastly, this study covered a narrower environmental gradient compared with e.g. Lammerts et al. (2001) who also included primary slacks and those with periodic saline influence, and included samples from the transitional areas between communities rather than focusing on homogenous stands of vegetation (e.g. Rodwell et al. 2000).

A potential issue for interpretation with respect to hydrological regimes is the temporal resolution of the hydrological data. Water level data available at monthly resolution in this study did not allow calculation of sum exceedance values, (i.e. the duration of time the water table is above or below thresholds for drought stress or water logging stress and the cumulative summation of that exceedence) which have been used to interpret plant species hydrological niches in other wetland ecosystems (Gowing et al., 1997). The water-holding capacity and soil permeability alter with organic matter content. As a result, the same water table depth below ground surface may differentially affect communities with different organic profiles and different mineralogy. It is also possible that there is a disconnect between water tables and plant responses in winter and summer, with groundwater levels in summer being less important than rainfall events which may re-wet surface layers and the rooting zone but do not contribute to recharge and therefore changes in water table. Nonetheless, despite these constraints, this study has for the first time identified the average hydrological regimes of a suite of Atlantic wet slack vegetation communities.

Relationships are based on hydrological data over a four-year period. This is an improvement on previous ecohydrological studies in the UK based on one or, at the most, two years hydrological data (Jones 1993; Ranwell, 1959), and is consistent with other studies. In Dutch dune slacks Noest (1994) found that 5-yearly means of a range of hydrological parameters provided better explanatory power on species’ distribution than the same parameters measured for the year of vegetation recording, or the previous year. In UK wet meadows, the best explanatory power for changes in vegetation is found for hydrological variables over the preceding three to seven year period: Sum Exceedence for waterlogging stress over a 3-year period proved effective for predicting shifts between vegetation communities (Gowing et al., 2005) whilst 5-7 year values for aeration and drought stress provide good explanatory power for stable community distributions (Gowing et al., 2002). In this study we make the assumption that the vegetation communities were in equilibrium with those hydrological conditions, but further work is required to establish variability in dune slack species assemblages between years and in response to changing hydrological regimes.

Dune groundwater levels are closely tied to climatic patterns and water levels vary considerably from one year to the next. The few long-running records available for the UK spanning several decades show large changes in average water tables, often over decadal scales (Davy et al., 2010; Robins and Jones, 2012). The net recharge to groundwater is strongly dependent on a fine balance between rainfall and evapotranspiration, and is as dependent on the timing of rainfall during the year as it is on total annual rainfall (Clarke and Sanitwong Na Ayutthaya, 2010). This makes dune slacks very sensitive to climatic changes. Studies on the impact of climate change on recharge to aquifers in the eastern UK suggest increasing recharge and water levels over the next few decades but becoming drier thereafter (Younger et al., 2002; Yusoff et al., 2002), while in Ireland, an overall decrease in effective run-off is predicted (Charlton, 2001). Clarke and Sanitwong Na Ayutthaya (2010) used the Darcian groundwater flow equation to model the movement of water through the dunes, which was then used to predict the effects of climate change. Their results suggested a drastic, long-term decline in water levels of more than 100 cm was highly likely at a west coast UK site. They also showed that climate change impacts on water tables were greater than impacts of afforestation or coastal change. Climate change impacts were a factor of two greater than the effects of sea level rise or afforestation, and an order of magnitude greater than the effects of rapid coastal erosion or accretion.

Although studies in the Netherlands have developed models to predict responses of Dutch dune species to groundwater change (von Asmuth et al. 2012; Witte et al. 2007; Geelen et al. 2004), no studies to date have quantified how changing water levels may affect dune vegetation communities in the UK. Findings from this study allow, for the first time, a projection of likely changes in vegetation communities under projected water level decline. Figure 6 shows frequency distributions of median water level for the main slack and dry dune grassland communities in this study plotted against water level projections to the 2080s for what is currently a wet slack type at Ainsdale (after Clarke and Sanitwong Na Ayutthaya, 2010). This suggests that towards the end of the 2030s conditions are no longer favourable for wet slacks and only dry slack community can persist. More worryingly, by the end of the 2050s it is likely that even dry slack communities will be replaced by dry dune grassland. Although in reality these communities are unlikely to replace each other sequentially (e.g. see Edmondson 1993 for a review of UK dune slack succession), it illustrates the severe shift in hydrological regimes that may occur and shows the implications for vegetation assemblages. These effects only take account of changes in water level. However changes in groundwater chemistry and the interaction with surface soil layers will also occur. Surface soil acidification, which is detrimental for the growth of basiphilous slack species, is a consequence of lowering water levels, due to a reduction in the seasonal replenishment of buffering capacity from base-rich groundwater (Sival and Grootjans, 1996). The diminution of winter flooding is likely to have direct impact on soil chemistry too, changing nutrient accumulation rates (Grootjans et al., 1991), redox processes (Sival and Grootjans, 1996), microbial cycles (Grootjans et al., 1996) and will consequently affect species interactions.

[Figure 6 about here]

The effects of climate change may be exacerbated by drainage or groundwater abstraction, and any form of water abstraction should be discouraged (Bakker et al., 2006; Davy et al., 2010; Grootjans et al., 1996; Van Dijk and Grootjans, 1993). In contrast, management techniques which encourage natural sand mobility may guarantee natural renovation of young successional stages, allowing the formation of new blowouts or creation of new secondary dune slack habitat through natural dune dynamics (Davy et al. 2010; Stratford et al., 2007). Other management methods used to improve mobilisation in sand dunes systems (such as sod cutting, removal of invasive scrubs, etc.) may be useful to alleviate detrimental effects of climate change in the absence of natural mobility (Kooijman, 2004).

5.Conclusions:

Atlantic dune slack assemblages can be characterised by their hydrological regime and soil parameters. However, there remains unexplained heterogeneity in the vegetation and the measured hydrological and soil parameters explain only 22.5% of observed variation. Assemblages separate broadly into wet slack, intermediate and dry slack types, with average winter water levels differing by around 20 cm between categories. Given the magnitude of these differences between community types, projected changes in water levels of over 100 cm due to climate change over the next few decades are a cause for concern. Hydrological regimes may shift completely from those currently associated with wet slacks to regimes currently found under dry dune grassland over a period of 50 years, and management options for responding to these changes should be explored urgently.

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Figure Legends:

Figure 1. Typical hydrographs showing monthly water levels at Newborough Warren over a four year period (2006-2009) for four dune slack communities and one dry grassland community (SD8) for comparison. y axis shows metres above ground level, zero represents ground surface.

Figure 2. PCA scores of the 245 quadrats, coded by vegetation community. The first three axes (Eigenvalues 0.13, 0.11, 0.06) explain 29.6% of the variance. See table 4 for full list of environmental variables.

Figure 3. CCA ordination analysis (a) distribution of environmental variables along first two axes, (b) distribution of quadrats grouped by NVC -core and transitional vegetation-, (c) distribution of quadrats representing core vegetation only, and distinguishing between SD14 subcommunities. See table 4 for a complete list of variables.

Figure 4. Average ion concentrations in soil, by vegetation community (core plus transitional vegetation) -bars represent SE-. a) anions; b) cations. Calcium is downscaled 10 times to be visualised with the other cations (e.g.: 1=10mg/100g dry soil).

Figure 5. Plot of hydrological niche occupied by three dune slack vegetation communities and dry dune grassland showing mean annual maximum (i.e. winter) and minimum (i.e. summer) water levels (metres above ground level, zero = ground surface), based on four-year hydrological regime (2006-2009). Thick inner lines indicate bounds of 67%ile of their distribution, thinner outer lines represent bounds for 90%ile. Dashed lines denote mean

annual maximum water levels for dry dune grassland based on quadrats surveyed in this study.

Figure 6. Frequency distribution curves of median water level for different slack types (data from this study, rescaled on 2nd y axis to max = 1), plotted against predicted changes in April water level (metres above ground level, 1st y axis) of a currently wet dune slack (SD15) at Ainsdale in north west England (after Clarke & Sanitwong Na Ayutthaya, 2010). Predicted April water levels show central estimate (thin black line), 75% confidence interval (dark grey zone) and 90% confidence interval (light grey zone).

Table 1: Locations and details of survey sites.

Site	Latitude, Longitude	Rainfall 1971-2000 l.t.a. (mm)	Dune area (ha)	Piezometers	Slacks surveyed	Quadrats
Newborough Warren	53°08′ N, 4°21′ W	830	529	49	46	212
Aberffraw	53°11′ N, 4°27′ W	830	248	2	2	12
Ainsdale	53°35′ N, 3°4′ W	870	508	3	3	9
Whiteford Burrows	51°38′ N, 4°14′ W	1110	142	4	4	12

Table 2: Summary of National Vegetation Classification communities and subcommunities identified in this study (adapted from Rodwell, 2000). Affinities with European vegetation associations in brackets.

NVC code	Name		Description
SD13	Sagina nodosa-Bryum pseudotriquetrum community (Saginion maritimae Westhoff, van Leeuwen & Adriani 1962, Samolo-Littorelletum Westhoff 1943)		**Early successional stage,** rich in bryophytes and liverworts. Usually with bare sand. **Fairly drought tolerant.**
SD14	Salix repens-Campylium stellatum Community (Junco baltici-Shoenetum nigricantis Westhoff 1946, Pyrolo-Salicetum Meltzer 1941)	(Caricion davallianae Kilka 1934)	Frequently species rich and associated with persistently **humid soils** and base-rich groundwater. Several rare species occur in this vegetation.
SD14b	Rubus caesius-Galium palustre subcommunity		Some of its constant species (Ranunculus flammula, Carex nigra) can indicate **tolerance to very wet periods.**
SD14c	Bryum pseudotriquetrum-Aneura pinguis subcommunity		**Young successional stage,** mosses have sparse cover, heliophilous and pioneer species can be present.
SD14d	Festuca rubra subcommunity		Characteristic of **drier substrates**, it can be an intermediate stage towards grass encroachment.
SD15b	Salix repens-Calliergon cuspidatum community Equisetum variegatum subcommunity (Equiseto variegati-Salicetum repentis Westhoff & Schaminèe 1995)		**Late successional stage**, generally species poor. Less dependent on base-richness of water, but strongly **related with flooding**.
SD16	Salix repens-Holcus lanatus Community (Salicion repentis arenariae Tüxen 1952)		**Late successional stage** in **dry slacks**. Dominated by fescue and grasses, forbs are still indicative of calcicolous substrate
SD17	Potentilla anserina-Carex nigra Community (Elymo-Rumicion crispi Nordhagen 1940)		Species composition reflects **damp habitat**, recalling fen meadows. Forbs-rich, with a sparse shrub cover.
SD8b	Festuca rubra-Galium verum Community Luzula campestris subcommunity (Galio-Koelerion, Westhoff and den Held 1969).		**Dune grassland** rich in dicotyledons characteristic of fixed sands. This vegetation has some affinities with a calcicolous sward.

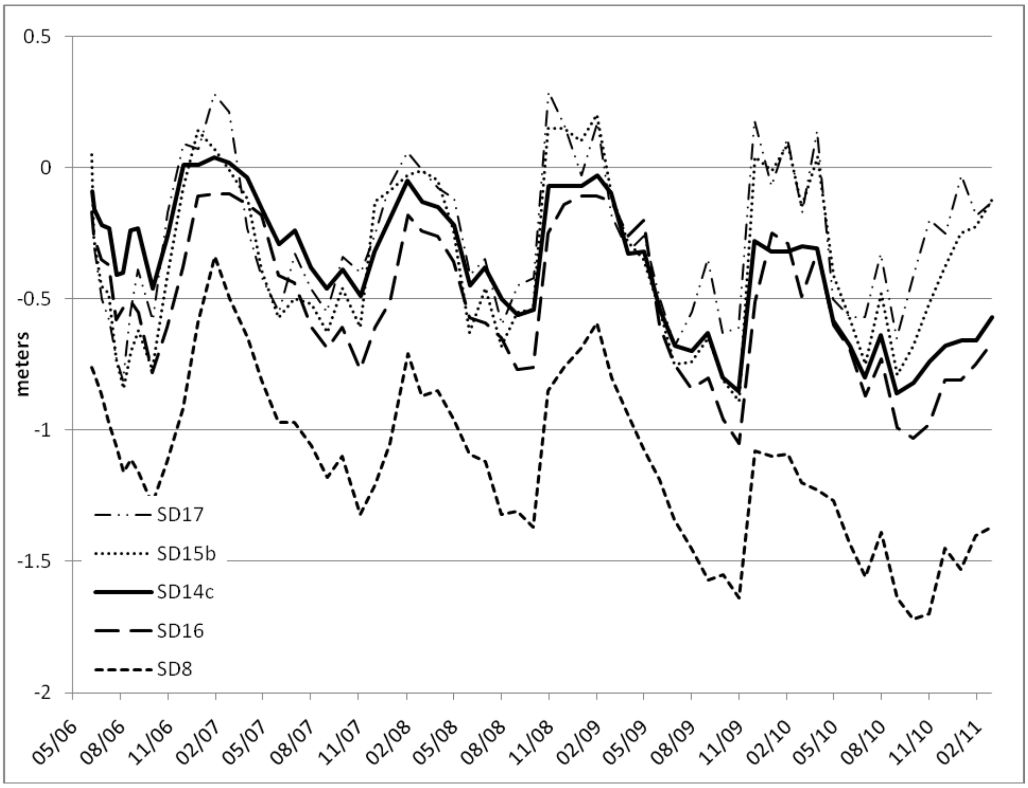
Table 3. Environmental variables used in vegetation analysis, showing percentage of total species variation explained within CCA and significance, when tested singly or in combination. *: significant at 0.05 level; **: significant at 0.01 level; *: significant at 0.001 level.**

	Variables	Variance explained (%)	Significance
Hydrological variables	Annual maximum water level (**Max**) (m)	6.3%	***
	Annual minimum water level (**Min**) (m)	3.8%	***
	Annual range (**Range**) (m)	2.0%	***
	Time flooding (**TiFlood**) weeks	0.8%	*
Soil variables	Soil moisture % (**Moist**)	6.3%	***
	LOI% (**LOI**)	4.1%	***
	pH	3.8%	***
	sulphate ($\mathbf{SO_4}^{2-}$) ppm	3.3%	***
	ammonium ($\mathbf{NH_4}^{+}$) ppm	3.1%	***
	sodium ($\mathbf{Na}^{+}$) ppm	2.4%	***
	chloride ($\mathbf{Cl}^{-}$) ppm	2.3%	***
	fluoride (**F**) ppm	2.3%	***
	phosphate ($\mathbf{PO_4}^{3-}$) ppm	1.4%	***
	magnesium ($\mathbf{Mg}^{2+}$) ppm	1.3%	***
	potassium ($\mathbf{K}^{+}$) ppm	1.1%	**
	nitrate ($\mathbf{NO_3}$) ppm	0.6%	n.s.
	calcium ($\mathbf{Ca}^{2+}$) ppm	0.5%	n.s.
Ellenberg indicators	Ellenberg F, N, R, L combined	21.2%	***
Combined models	Hydrological parameters (**Max** + **Min** + **Range** + **TiFlood**)	8.9%	***
	Key hydrological + soil parameters (**Max** + **pH** + **Moist**)	12.9%	***
	Extended hydrological + soil parameters (**Max** + **Moist** + **pH** + $\mathbf{NH_4}$ + $\mathbf{PO_4}$)	14.6%	***
	All variables	22.5%	***

Table 4: Summary environmental parameters for core quadrats (n=139) and core plus transitional quadrats (n=233), SD8 excluded. Values for each variable are expressed as mean ± standard error, brackets show minimum and maximum values for each community. Hydrological parameters are calculated averages over 4 years. For each variable, lower case letters denote significant differences between community types using core quadrats only, upper case letters for tests using core plus transitional quadrats.

		CORE GOOD QUALITY VEGETATION					CORE AND TRANSITIONAL VEGETATION			
	NVC / **VARIABLE**	**SD15b** n=15	**SD14b** n=28	**SD14c** n=47	**SD14d** n=35	**SD16** n=14	**SD17** n=7	**SD15** n=32	**SD14** n=165	**SD16** n=29
WATER LEVEL (m)	**average Minimum**	-0.61 ±0.020^{a} (-0.69 , -0.51)	-0.62 ±0.016^{a} (-0.78 , -0.53)	-0.70 ±0.020^{ab} (-0.90 , -0.41)	-0.75 ±0.014^{b} (-0.88 , -0.62)	-0.98 ±0.059^{c} (-1.57 , -0.81)	-0.75 ±0.034^{A} (-0.85 , -0.58)	-0.64 ±0.015^{A} (-0.79 , -0.51)	-0.73 ±0.014^{A} (-1.41 , -0.41)	-0.98 ±0.050^{B} (-1.57 , -0.77)
	average Maximum	0.21 ±0.018^{a} (0.12 , 0.29)	0.17 ±0.027^{a} (-0.07 , 0.32)	0.00 ±0.022^{b} (-0.21 , 0.22)	0.02 ±0.016^{b} (-0.12 , 0.18)	-0.25 ±0.061^{c} (-0.82 , -0.02)	0.09 ±0.032^{AB} (-0.01 , 0.25)	0.16 ±0.020^{A} (-0.09 , 0.29)	0.02 ±0.014^{B} (-0.48 , 0.32)	-0.22 ±0.043^{C} (-0.82 , -0.02)
	average Range	0.81 ±0.008^{ab} (0.77 , 0.85)	0.80 ±0.013^{a} (0.70 , 0.85)	0.69 ±0.015^{b} (0.49 , 0.85)	0.77 ±0.007^{a} (0.70 , 0.83)	0.72 ±0.016^{ab} (0.63 , 0.80)	0.84 ±0.005^{A} (0.83 , 0.85)	0.79 ±0.009^{AB} (0.70 , 0.85)	0.74 ±0.008^{B} (0.49 , 1.02)	0.76 ±0.023^{BC} (0.63 , 1.02)
SOIL	**Moisture (%)**	33.6 ±1.68^{a} (19.9 , 43.7)	29.8 ±1.06^{ab} (17.9 , 41.6)	18.1 ±0.76^{c} (7.2 , 33.8)	25.4 ±1.42^{b} (12.4 , 60.7)	15.4 ±1.52^{c} (7.5 , 25.0)	34.8 ±2.86^{A} (19.8 , 44.3)	36.4 ±1.46^{A} (19.9 , 63.7)	23.6 ±0.61^{B} (7.2 , 60.7)	17.4 ±1.05^{C} (5.7 , 28.5)
	LOI (%)	7.2 ±0.37^{a} (3.8 , 9.5)	5.1 ±0.38^{bc} (0.9 , 10.8)	2.6 ±0.17^{d} (0.6 , 5.5)	5.8 ±0.42^{ab} (3.0 , 18.4)	3.6 ±0.30^{cd} (1.5 , 6.0)	8.9 ±0.77^{A} (5.8 , 11.9)	8.2 ±0.55^{A} (3.8 , 17.9)	4.38 ±0.18^{B} (0.6 , 18.4)	4.3 ±0.24^{B} (1.4 , 6.6)
	pH	7.1 ±0.17^{c} (6.2 , 8.1)	7.8 ±0.10^{ab} (6.3 , 8.6)	8.2 ±0.04^{a} (6.9 , 8.7)	7.1 ±0.11^{c} (6.0 , 8.1)	7.5 ±0.15^{bc} (6.5 , 8.3)	6.3 ±0.17^{C} (5.8 , 7.0)	7.0 ±0.12^{BC} (5.9 , 8.2)	7.7 ±0.05^{A} (6.0 , 8.7)	7.4 ±0.12^{B} (6.0 , 8.3)
% cover	**Bare ground**	0.1 ±0.13^{ab} (0 , 2)	0.4 ±0.25^{b} (0 , 6)	4.2 ±1.18^{a} (0 , 40)	0.0 ±0.00^{b} (0 , 0.1)	2.2 ±1.8^{ab} (0 , 25)	2.6 ±1.19^{A} (0 , 8)	0.1 ±0.06^{B} (0 , 2)	2.0 ±0.46^{A} (0 , 40)	1.4 ±0.93^{AB} (0 , 25)
	Litter	1.9 ±0.73^{a} (0 , 10)	0.4 ±0.22^{b} (0 , 5)	0.4 ±0.12^{b} (0 , 4)	0.4 ±0.20^{b} (0 , 6)	0.7 ±0.48^{ab} (0 , 5)	28.6 ±14.2^{A} (0 , 90)	3.5 ±1.88^{B} (0 , 60)	1.3 ±0.49^{B} (0 , 60)	2.6 ±1.43^{B} (0 , 40)

Figure 1.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SD8
05/06
08/06
11/06
02/07
05/07
08/07
11/07
02/08
05/08
08/08
11/08
02/09
05/09
08/09
11/09
02/10
05/10
08/10
11/10
02/11

Figure 2.

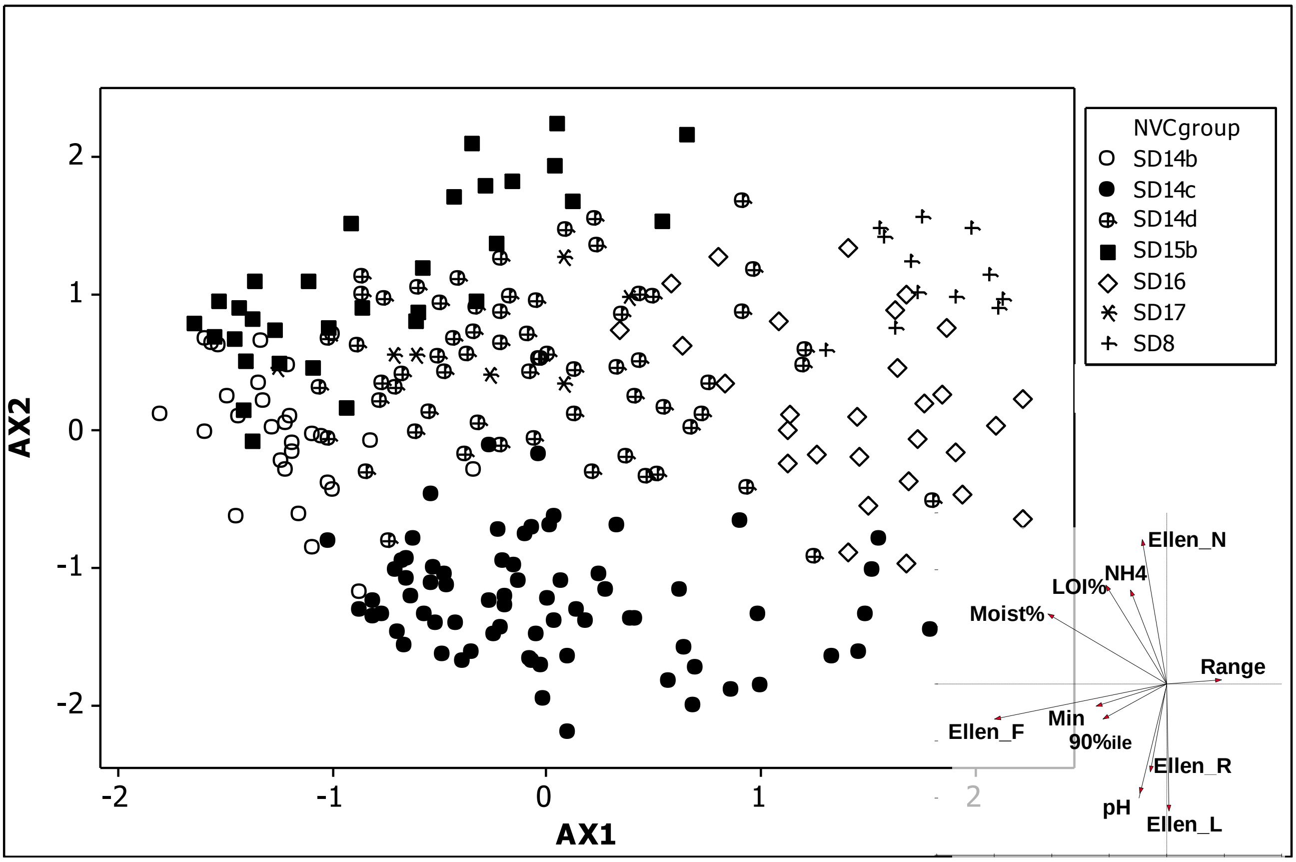
AX2
AX1
2
1
0
-1
-2
-2
-1
0
1
2
NVCgroup
○ SD14b
● SD14c
⊕ SD14d
■ SD15b
◇ SD16
✳ SD17
+ SD8
Ellen_N
NH4
LOI%
Moist%
Range
Ellen_F
Min
90%ile
Ellen_R
pH
Ellen_L

Figure 3.

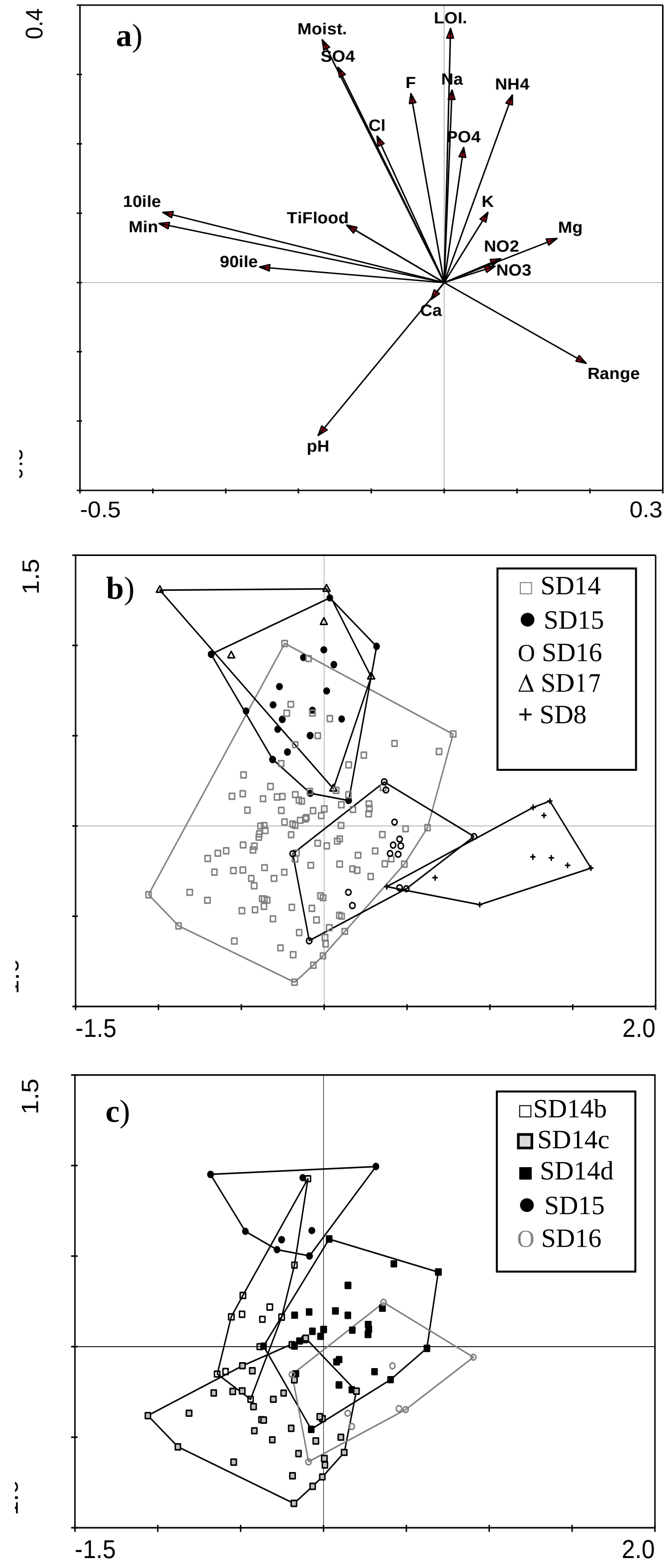
a)
0.4
-0.5
0.3
Moist.
SO4
LOI.
F
Na
NH4
Cl
PO4
K
Mg
10ile
Min
TiFlood
90ile
NO2
NO3
Ca
Range
pH
b)
1.5
-1.5
2.0
□ SD14
● SD15
O SD16
Δ SD17
+ SD8
c)
1.5
-1.5
2.0
□SD14b
▣SD14c
■ SD14d
● SD15
O SD16

Figure 4.

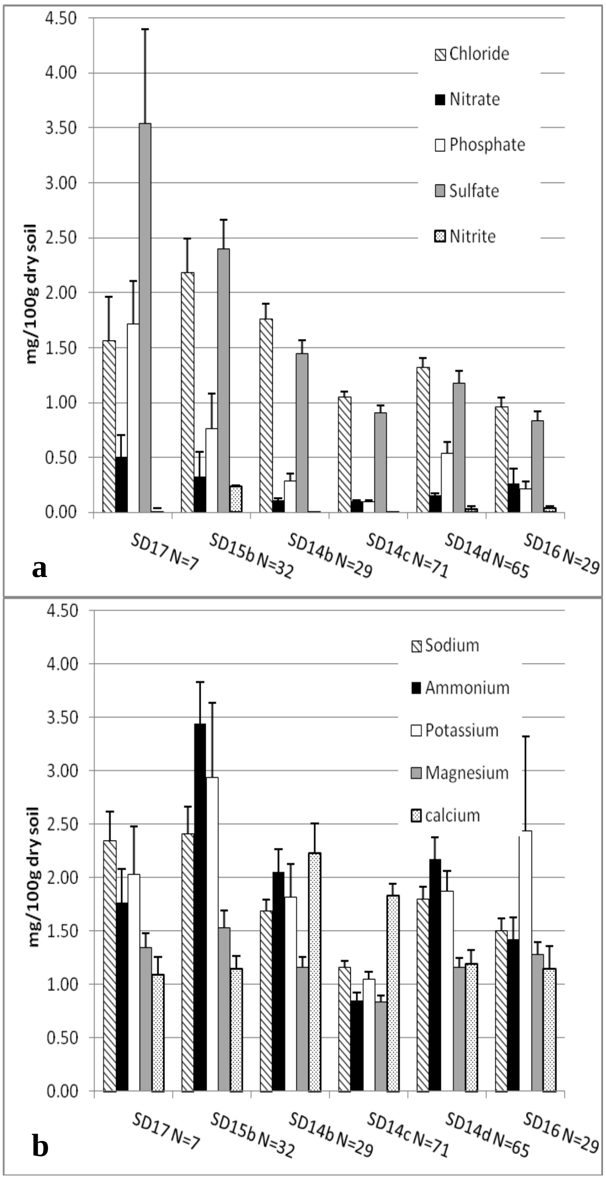
mg/100g dry soil
4.50
4.00
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
Chloride
Nitrate
Phosphate
Sulfate
Nitrite
SD17 N=7
SD15b N=32
SD14b N=29
SD14c N=71
SD14d N=65
SD16 N=29
a
mg/100g dry soil
4.50
4.00
3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
Sodium
Ammonium
Potassium
Magnesium
calcium
SD17 N=7
SD15b N=32
SD14b N=29
SD14c N=71
SD14d N=65
SD16 N=29
b

Figure 5

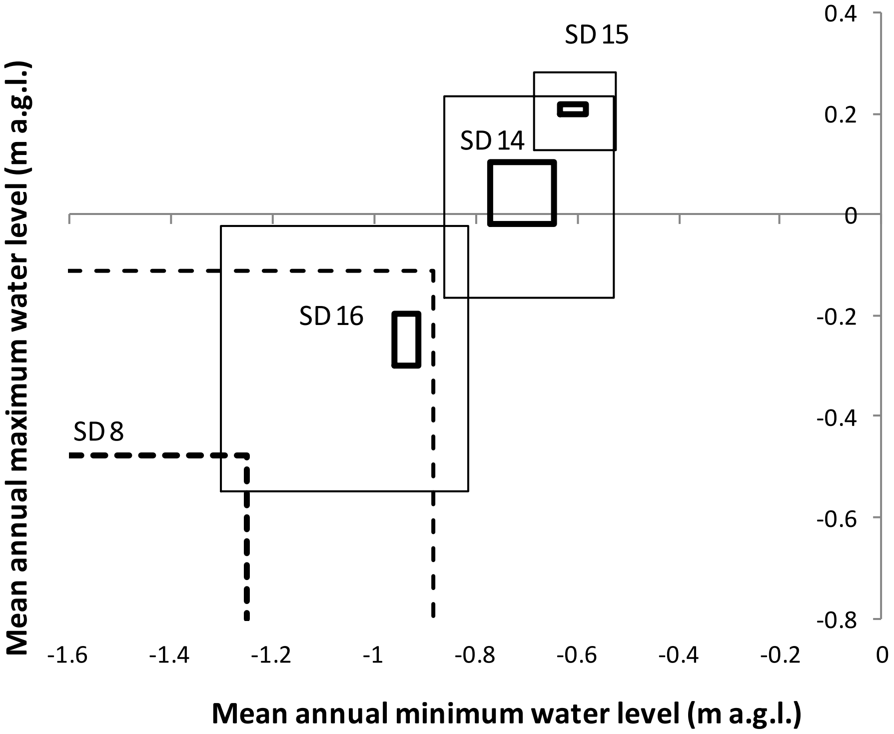

Figure 6