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Factors controlling soil development in sand dunes: evidence from a coastal dune soil chronosequence.

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Abstract
Aerial photographs, maps and Optically Stimulated Luminescence dates were combined with existing soil data to construct high resolution chronosequences of soil development over 140 years at a temperate Atlantic UK dune system. Since soil formation had progressed for varying periods under different climate and nitrogen deposition regimes, it was possible to infer their relative influence on soil development compared with location-specific variables such as soil pH, slope and distance to the sea.
Results suggest that soil development followed a sigmoid curve. Soil development was faster in wet than in dry dune habitats. In dry dunes, rates were greater than in the literature: they increased with increasing temperature and nitrogen deposition and decreased with increasing summer gales. The combination explained 62% of the variation. Co-correlation meant that effects of nitrogen deposition could not be differentiated from temperature. In wet dune habitats, rates increased with temperature and decreased with gales. The combination explained only 23.4% of the variation; surprisingly, rainfall was not significant. Effects of location-specific variables were not significant in either habitat type. Nitrogen accumulation was faster in wet than dry dune habitats, averaging 43 $kg.N.ha^{-1}.yr^{-1}$ overall. Nitrogen accumulation greatly exceeded inputs from atmospheric deposition, suggesting rates of input for biological N fixation are 10 - 60 $kg.N.ha^{-1}.yr^{-1}$.
Recent climate and/or nitrogen deposition regimes may have accelerated soil development compared with past rates. These data suggest the importance of changing climate on soil development rates and highlight the contribution of biological N fixation in early successional systems.

Abbreviations:
OSL – Optically Stimulated Luminescence
%LOI – percentage loss on ignition
PCA – Principal Components Analysis

Introduction

Dune systems exhibit successional development of plant communities and soil, representing the earliest stages of soil development. If dunes can be accurately aged, they are useful as a model system for studying the basic processes governing soil development, and in particular the balance between climate effects and local factors.

Soil development is broadly controlled by three principal factors: climate, the soil parent material, and vegetation type. Temperature and rainfall exert a major influence on soil development. Rainfall drives leaching rates and the rate of decalcification (Wilson 1960). Together they govern rates of plant growth, with the balance between rainfall and evaporation being particularly important in dune systems (Sevink 1991). Both temperature and soil moisture exert complex controls on the rate of decomposition of organic matter (McLaren and Cameron 1990), with slower decomposition and therefore faster soil development generally occurring in wetter and in cooler environments. Vegetation type also plays a role. The chemical composition of plant litter, particularly the C:N ratio and the quantity of recalcitrant compounds such as lignin and complex organic molecules strongly affect rates of decomposition (Berg et al. 1998; O'Neill and Norby 1996), while plant productivity controls the supply of organic matter to the soil. Most semi-natural systems, and particularly early successional systems, are nitrogen limited (Vitousek et al. 1997), although phosphorus limitation can also be important in calcareous dune systems (Kooijman and Besse 2002; Kooijman et al. 1998). Where nitrogen is the primary limiting nutrient, additional supply increases plant productivity (Berendse 1998) and reduces the C:N ratio of litter which usually acts to speed up mineralisation rates (Berendse 1998). However, the long term effects of N on soil development are poorly understood. Other factors more intrinsic to rates of soil development in younger dune soils include the height above the water table - leading to great differentiation between soil development rates in dry dunes and rates in dune slacks, the initial carbonate content of the sand, the frequency of disturbance, the management regime, climate factors such as windspeed and direction and physical factors which modify microclimate such as slope and aspect (Gerlach et al. 1994; Grootjans et al. 1998). While all these factors affect soil development, the balance between broad-scale and local influences on soil development is poorly understood.

Soil development is a slow process and is not easily directly measured. Soil development is typically studied through chronosequences, over timescales ranging from a few decades (Berendse et al. 1998; Ernst et al. 1996; Lammerts et al. 1999; Olff et al. 1993) to hundreds (Gerlach et al. 1994; Salisbury 1922; 1925; Wilson 1960) and even thousands of years (Olson 1958a; b; Syers et al. 1970). Types of chronosequence available in dunes include sampling landforms resulting from successive phases of dune mobility, successive dune ridges laid down on prograding coasts (Salisbury 1925; Wilson 1960) and chronosequences following disturbance at known time points, for example turf stripping episodes in dune slacks in the Netherlands (Berendse et al. 1998; Ernst et al. 1996; Lammerts et al. 1999). Such chronosequences provide valuable information about soil development over time, particularly when backed up by independent dating methods, but also have limitations. Old dune landforms are prone to subsequent disturbance or partial re-mobilisation, soil development over time on accreting coasts is partially confounded by increasing distance from the sea as the shoreline progrades, while chronosequences following management often inherit a residual elevated organic matter or soil nutrient content, or soil decalcification (Berendse et al. 1998), and hence do not truly re-set the clock.

High resolution aerial photography, available since at least the 1940s for many areas as a result of military activity in the Second World War, allows ages of younger soils to be estimated fairly accurately given a sufficiently detailed photographic record, while the age of older soils can be estimated using conventional historical records and dating techniques. This gives a much greater temporal and spatial resolution to the very early stages of soil development. Since soils of different ages will have experienced different climate and nitrogen deposition regimes (Berendse et al. 1998) in principle it allows inferences to be made about the factors governing soil development at one site which would only otherwise be possible comparing a wide range of sites across a climosequence where it is difficult to control for the influence of other factors such as mineralogy, sand supply, etc. and to accurately determine soil ages.

In order to address the lack of studies focusing on soil development and climate in relatively young dune soils (Sevink 1991), a detailed chronosequence of soil development was created for a dune system in North Wales, extending to 140 years. The chronosequence was then used to address the following hypotheses. Does soil development proceed faster during periods with cooler, wetter average climate conditions? Does soil development proceed faster under higher levels of nitrogen deposition? Does small scale variation in location-specific physico-chemical factors exert a greater influence on soil development than large-scale factors such as climate and N pollution. Lastly, the implications for N and C accumulation in early successional systems are discussed in relation to these findings.

Materials and methods

Overview

This analysis uses data collated under a combination of published and unpublished studies for which soil data and accurate soil sampling locations were available for Newborough Warren, a large dune system in North Wales, United Kingdom (Emmett 2007; Jones et al. 2002; Jones et al. 2004). These data were supplemented by additional sampling of under-represented habitats across a range of soil ages as part of this study, giving 90 data points overall with a reasonable geographical spread across the dune complex, and covering the full range of available habitats from younger to older dry dune habitats (42 samples) including mobile and semi-fixed dunes and dune grasslands, and younger to older wet dune habitats (48 samples) including dune slacks and damp dune grasslands. In dune systems, soil formation consists primarily of the accumulation of organic matter and lacks the accumulation of material from weathering of bedrock. Therefore, in this study, the degree of organic matter accumulation is used as the measure of soil development, calculated as percentage loss on ignition (%LOI).

Site description

Newborough Warren is one of the largest UK dune systems, located on the island of Anglesey, North Wales, UK (53:08N 4:21W). It is up to 2 km wide and approximately 1300 hectares in area, half of which was planted with forest over the period 1949 – 1969. Within recent history the dune system has been highly mobile, with approximately 75 % bare sand in the 1950s, and has progressively stabilised since then with only 6 % bare sand in 1991 (Rhind et al. 2001; Rhind et al. 2007). The site contains a number of dune ridges with intervening dune slack areas and sand plains which presumably formed during different episodes of mobility. However, aerial photographs show that most of these surfaces were almost completely mobile in the 1940s with established vegetation limited to dune slacks, and fixed dune grasslands at the edge of the site and in smaller discrete patches across the site. Soil and vegetation development has proceeded patchily across the site since the major onset of stabilisation in the early 1940s, and reflects local variability in the time of establishment rather than a clear succession of habitats of increasing age away from the sea.

Collection and preparation of soil samples:
Soil samples from all the previous studies had been collected using the same methodology; taking 5 cm diameter soil cores down to a depth of 15 cm. Supplementary field sampling for this study utilised the same method. Samples were collected in 2002 and 2006, with supplementary sampling conducted in 2007. In the laboratory, samples were homogenised and large roots, shells and stones removed. Soil moisture and percentage Loss on Ignition (%LOI) were determined at oven temperatures of 105 °C and 375 °C respectively for 16 hours (MAFF 1986). The oven temperature of 375 °C is sufficient to combust organic matter without dissociating too much carbon dioxide from the carbonates (Ball 1964). Total carbon and nitrogen contents in the original studies were measured by combustion on a Carlo Erba CSN analyser, after acidification to remove carbonates.

Estimating soil age
Ages for soil sampling locations were established using a variety of methods including aerial photographs, Ordnance Survey maps and optically stimulated luminescence (OSL) dated soils. The data sources and methods are described briefly here but are available in greater detail in Jones et al. (2007). For the younger soils (1940s onwards), aerial photographs were used to establish when vegetation cover at each location commenced. A high temporal-resolution sequence of aerial photographs was available for Newborough Warren, predominantly at a scale of 1:10,000, with some at coarser scale. Soil sample points (GPS co-ordinates ± 10 m) were matched to locations on ortho-rectified photographs with the aid of available information about the slope, aspect, habitat type and bare sand cover from the associated survey data. Locations were then traced back over time using the full sequence of individual photographs, back to 1945, to identify the progressive colonisation of vegetation. Vegetation cover at each sampling location was estimated to the nearest 10 %, with bare sand scored as 0 % vegetation cover. The high temporal resolution of the aerial photography record allowed most ages to be estimated to within 5 or 10 years, with T=0 for soil development taken as the mid-point date between the aerial photographs when vegetation cover was first apparent on the bare sand, with the dates of the photographs providing bounds for the age estimate.

Minimum ages of older soils (pre 1940s) were estimated using Ordnance Survey maps (1:9600), surveyed in 1887, and revised in 1899 and 1915. A more precise age for one area of fixed dune grassland was available from an OSL dating study (Bailey 2004). OSL dates the sand below the organic layer, giving a maximum age in this case of 145 ± 15 yrs, which was assigned to all points in the contiguous fixed dune grassland near that location.

General factors affecting soil development: Climate and nitrogen deposition
A subset of the data (14 dry and 40 wet habitat samples) was prepared covering the period of most rapid soil development. These samples included only those for which reliable age estimates were available, based on the photographic record, and exclude all other samples including the older OSL dated samples. Accumulation rates, expressed as %LOI accumulation per year were calculated over the period between reaching 100 % vegetation cover and when the soil was sampled, in order to compare rates of organic matter accumulation for each data point over time. For each soil sample point, climate variables and N deposition were averaged over the same period of soil development. Monthly climate records going back to 1941 were available for a Royal Air Force Station at Valley, a coastal site 17 km to the north west, and the following climate variables were assessed: Average annual rainfall, average, maximum and minimum daily air temperature, number of frost days,

average windspeed, number of days with gale force winds, and Talbot's Mobility Index (Mo) (Talbot 1984), which combines information about windspeed, rainfall and temperature to indicate how favourable the conditions are for dune mobility. Where relevant (for rainfall, air temperatures, frost days and gale days), these variables were further broken down to 6-month summer (Apr - Sept) and winter (Oct - Mar) periods, and to 3-month spring (Mar – May), summer (Jun – Aug), autumn (Sept – Nov) and winter (Dec – Feb) periods in order to further determine which seasonal climate variables correlate most strongly with soil development. Atmospheric nitrogen deposition was reconstructed back to 1941 as follows. A generic historical reconstruction profile of NH_y and NO_x deposition for the UK (Fowler et al. 2004) was parameterised for Newborough Warren using oxidised and reduced nitrogen deposition data from Mohd-Said (1999) and unpublished CEH data. While the generic reconstruction predicts a decrease in deposition after 1990, recent measurements of NH_3 concentration at Newborough (CEH, unpublished data) suggest a slight increase. Therefore, in the absence of detailed measurements the deposition profile used here beyond 1999 assumes continuation of 1999 levels.

Location-specific factors affecting soil development, physical, chemical and biological parameters.
In order to examine the effect of location specific factors on soil development for the same subset of data, associated data where available were collated for each soil sampling location. These included: distance to the sea in the direction of the prevailing winds, calculated in a GIS, soil pH measured in both water and $CaCl_2$, and slope of the terrain (degrees).

Data analysis and statistics.
Soil development curves were prepared by plotting percentage loss on ignition (%LOI) against soil age. Ages estimated from aerial photographs used the mid-point of the photograph interval, with error bars denoting the age bounds. Older soils with uncertain ages were plotted as minimum estimated age, with a nominal 20-year error bar. OSL dates from Bailey (2004) were reported ± 15 years, but as they represent a maximum age they are given a nominal 20-year error bar denoting a possible younger age.

When analysing factors affecting rates of soil development, relationships between %LOI yr^{-1} and climate and location-specific environmental variables were assessed using linear regression against individual variables. Collinearity between variables was explored using principal components analysis (PCA) and multiple linear regression. Nitrogen accumulation rates were calculated from soil N pool data in the original studies. The PCA and all statistical tests were conducted in Minitab v 14.1.

Results

Soil curves
The data were separated into dry dune habitats (mobile, semi-fixed and dry fixed dune grasslands) and wet dune habitats (dune slacks and damp dune grassland) based on the vegetation assemblages recorded when the soil samples were taken. Quadrat data were classified according to the UK National Vegetation Classification (Rodwell 2000) using the MATCH programme (Malloch 1998). Dry and wet habitats were separated because the rates of soil development differ strongly between dry and wet habitats due to the influence of the water table on winter flooding duration and water availability in summer.

The organic matter accumulation data produce sigmoid curves which go through three main phases: a slow increase in %LOI, followed by a period of rapid increase, then a levelling off

of %LOI to a much slower rate of increase. A similar pattern is observed in both dry and wet dune habitats, although with different characteristics.
In the dry habitats (Figure 1a), the initial phase consists of a slow increase in %LOI from a starting point of around 0.2 % in the bare sand of mobile dunes to around 1 % occurring more or less when vegetation cover reaches 100 %. Analysis of all data points, including those later becoming fully fixed, shows that the average time taken to become fully vegetated is 22.3 ± 15.2 years in these dry dune habitats (intervals ranged from 4 to 56.5 years). The second, steeper phase commences roughly when full vegetation cover is established and the organic layer exceeds 1 cm thickness (data not shown). The %LOI increases rapidly and by 60 years after the onset of vegetation establishment some soils have reached organic matter contents comparable to the much older soils. In the third phase, the OSL dates and the estimated minimum ages of the older fixed grassland soils suggest that %LOI then appears to level out, with values of around 3 – 4 % in the oldest dune soils at this site, with a maximum organic layer thickness of 6 cm (data not shown – two outlier samples reach 8.5 cm due to smearing of the soil profile by slow sand accumulation, however %LOI values for these samples are not outliers).

The curve for the wet habitats (Figure 1b) shows the same overall pattern but the rate of increase is steeper and reaches higher organic matter contents. Here the initial phase is almost absent and dune slacks take on average only 11.3 ± 7.8 years to become fully vegetated, around half the time taken in the dry dune soils. Some soils under 60 years old reach values of 4 – 5 %LOI and, as with the dry dune habitats, there is considerable scatter around the steeper part of the curve. Our knowledge of the shape of the curve beyond an age of 60 years is constrained by the availability of historical records with which to accurately date soil locations, and in particular the older dune slacks within the Warren. However, the data from the OSL-dated damp grasslands at this site suggest that a similar plateau exists in wet dune soils, this time at higher LOI values of 5 – 7 %, although this level may be higher still since wet dune slacks generally have a higher organic matter content than damp grassland. The maximum organic layer thickness was 9 cm (data not shown).
These soil development curves were compared with other data available from the literature. For dry dune habitats (Figure 2), it is apparent that the curve is both steeper and reaches a higher %LOI before levelling off in comparison with other published data. In the wet dune habitats (Figure 3), to aid comparison with published studies, the data for Newborough were converted to organic matter pools using bulk density data from the original studies. In contrast to the dry dune habitats, the resulting soil development curve reaches a lower organic matter content and is less steep than data reported for Terschelling in the Netherlands.

Climate variables and nitrogen deposition
Analysis of some of the general and location-specific factors affecting rates of organic matter accumulation was undertaken by regression of accumulation rates against climate and location-specific environmental variables for soils under 60 years old for which soil age was reliably estimated; soil ages ranged from 11 to 57.5 years. The trends in the main climate variables at Newborough are presented briefly to provide context for the analysis. Average temperature (Figure 4a), and maximum and minimum temperatures (not shown) showed similar trends over time, with an increasing temperature trend particularly over the last 20 years; all were included in the analysis in case biological responses were linked to temperature thresholds such as growing season temperatures. The number of frost days (not shown) was also included in the analysis and showed marked differences in pattern when broken down to 3-month seasons. The profile for reconstructed nitrogen deposition at Newborough (Figure 4a) showed a continuous increase over time to a peak in the 1990s

which is more-or-less maintained subsequently. Rainfall (Figure 4a), shows considerable inter-annual variation but is highest in the period 1940 - 1970. However, when broken down to 3-month seasons (Figure 4b), clear seasonal differences in the rainfall pattern emerge. Peaks and troughs in rainfall occur over time periods of 2 – 10 years, but are not consistent by season. For example, a peak in summer rainfall in the late 1950s is offset from peaks in autumn and winter rainfall by around 3 years, while spring rainfall records a trough over the same period. Long-term trends suggest declining summer and winter rainfall, contrasted with increasing spring and autumn rainfall. The number of gale days (Figure 4c) shows generally low values until the early 1960s when they increase rapidly over a five-year period and then steadily decline again. As with rainfall, the number of gale days show distinct differences when broken down by 3-month season. Talbot's Mobility Index and average windspeed (not shown) show broadly similar trends to that of winter gale days, but with stronger declines in the 1960s and 1990s. Figure 5 shows the inter-relationships between the climate and N deposition variables in a principal components analysis. Nitrogen deposition is strongly associated with all the temperature variables which form a cluster high on axis 1, while frost days form a looser cluster low on axis 1. Rainfall and gales by season show the greatest variability and exhibit relatively little clustering. Figure 6 shows the relationship between soil age and the %LOI accumulation rate, and indicates high variability in %LOI accumulation per year.

Table 1 shows the results of the regression of individual variables against the %LOI accumulation rate. In the dry dune habitats, temperature variables explain a high proportion of the variance, with R^2 ranging from 26.0 % up to 48.8 %. Surprisingly, the relationship is positive with greater %LOI yr^{-1} at higher temperatures. Average, maximum and minimum temperatures all behave similarly, with results from both 6-month and 3-month seasons suggesting that winter temperatures are less important than the other seasons. The number of frost days also explains a high proportion of the variation (R^2 up to 43.9 %). Consistent with the temperature results, frosts are less important in winter than in other seasons and the negative relationship shows that %LOI yr^{-1} is higher with fewer frost days. Total annual rainfall has relatively low explanatory power, although there is a significant negative relationship with 6-month summer rainfall, suggesting %LOI yr^{-1} is positively influenced by drier summers. Similarly there is a weakly significant negative relationship with the number of gales in 6-month summer. Neither wind speed nor Talbot's Mobility Index appear to influence the rate of soil development. However, nitrogen deposition shows a strong positive relationship, explaining 42.0 % of the variation.

In the wet dune habitats, a lower proportion of the variation is explained by any of the variables than in the dry dune habitats. Temperature influences soil development to a much lesser extent than in the dry dunes, explaining at most 11.9 % of the variation. In contrast to the dry dunes, winter temperatures show the strongest relationship with %LOI yr^{-1}, with 3-month winter temperatures having the greatest influence. Again the relationship is positive, showing greater %LOI yr^{-1} at higher average winter temperatures. The negative relationship with frost days confirms this pattern, with 3-month winter frosts explaining 14.4 % of the variation. Rainfall explains very little of the variation. However, the number of gale days show some significant negative relationships, with 3-month spring and autumn seasons being most important. Neither windspeed, Talbot's Mobility Index nor nitrogen deposition explain a significant proportion of the variation in %LOI yr^{-1} in wet dune habitats.

Location-specific environmental variables
Of the location-specific variables in the dry dune habitats soil pH explains up to 28.8 % of the variation in %LOI yr^{-1} but this is not significant due to the lower number of samples with associated pH information. Neither distance to the sea nor slope steepness significantly explain any of the variation. In the wet dune habitats, neither pH nor distance to the sea explain much variation. All dune slack samples were taken on flat ground, so slope could not be analysed as an explanatory variable for the wet dune habitats.

In addition to the multivariate analysis, multiple regression analysis was used to determine the degree of co-correlation between variables. In the dry dunes, temperature showed the strongest positive relationship with %LOI yr^{-1}, but when other significant variables were added there was little additional explanatory power (only average temperature was used since maximum and minimum temperatures were assumed to be highly co-correlated with average temperature). It made little difference whether the 6-month seasonal variables were used or the highest explanatory (usually 3-month) seasonal variable in each climate variable set. Although strongly significant on its own, N deposition appears to be highly co-correlated with temperature. Environmental variables that were partially orthogonal to temperature and which helped explain additional variation in the dry habitats included number of gale days and summer rainfall, with temperature (AveTemp_Aut3) and gale days (Gales_Sum6) together explaining well over half the variation (R^2 of 62 %). In the wet habitats, although there was a high degree of co-correlation of both average temperature and frost days with the number of gale days, when combined in a multiple regression these three variables (AveTemp_Win3, Gales_Spr3 and Frost_Win3) explained 23.4 % of the variation.

While the location-specific environmental variables ought not to be co-correlated with climate variables they added only a little explanatory power. The proportion of the variation explained increased to 68.4 % in the dry dunes when slope was added as a variable. In the wet dune habitats the variation explained increased to 27.5 % when distance to the sea was combined with the above three climate variables.

Nitrogen and carbon accumulation rates
Nitrogen accumulation rates (Figure 7) show considerable variation in this dataset, ranging from 16 - 67 kg N ha^{-1} yr^{-1}. Average values (± s.d.) are lower in the dry dunes (37.6 ± 13.1 kg N ha^{-1} yr^{-1}) than the wet dune habitats (45.8 ± 15.0 kg N ha^{-1} yr^{-1}). Figure 7 suggests a negative trend of N accumulation rate with soil age, but the trend is not significant (R^2 = 5.5 %, p = 0.231 for dry and wet habitats combined). Carbon accumulation rates are 582 ± 262 kg C ha^{-1} yr^{-1} in the dry dunes and 730 ± 221 kg C ha^{-1} yr^{-1} in the wet dune habitats.

Discussion
This paper presents a detailed chronology over the first 140 years of soil development in sand dune habitats at Newborough Warren. Soil development, taken as organic matter accumulation, is non-linear and shows strong correlations with climate variables, in particular temperature and the number of gales, while location-specific variables appear to have less influence.

This study has, for the first time, produced a highly detailed chronology of the first 60 years of soil development in dry and in wet dune habitats, extending with a lower temporal resolution to 140 years. The data suggest that soil development is strongly non-linear and follows a sigmoid curve. Data from the literature for dry dune habitats suggest either a linear or increasing rate over a period of 200 years or so (Gerlach et al. 1994; Salisbury 1922; 1925; Wilson 1960), but lack the high resolution at this early part of the curve. In wet dune habitats, a sigmoid curve appears to be the norm (Berendse et al. 1998; Ernst et al. 1996; Lammerts et al. 1999). However, the greater resolution provided in this study suggests that a sigmoid curve applies to both habitat types. The initial slow start reflects the time taken for full vegetation cover to establish, when litter fall and root carbon inputs are sufficient to commence the build-up of organic matter. Although it may seem obvious that soil development progresses faster under full vegetation cover, it has strong implications for the management of dune systems, as it suggests that soil development can be retarded if the semi-fixed areas can be maintained in an open state. At the upper end of the curve, the reasons for the slow down in rates of soil development are less obvious. Soil chronosequences over much longer time periods show a continuously decreasing rate of organic matter accumulation, until equilibrium with climate conditions is achieved. This can take up to 10,000 years (Syers et al. 1970). However, a very rapid change in accumulation rate is shown in the first 100 years of this chronosequence. This is not an artefact of the sampling methodology as the organic layer thickness did not exceed the 15 cm sampling depth in any sample. The rate of organic matter accumulation in dune soils reflects the balance between supply of organic material and its decomposition. Historically in the UK, the hind dune grasslands have been used as marginal grazing, but are also heavily grazed by rabbits (Boorman 1989). Thus the slow down in organic matter accumulation observed at around 60 years may reflect a decrease in the supply of organic matter due to off-take by grazers (Ritchie et al. 1998). There may also be changes in decomposition rate, since skeletal soils such as these lack a true soil profile and the full range of decomposer guilds may not be functionally present. Decomposition in very young sand dune soils is primarily by microbial and fungal decomposers rather than macrofauna (McLachlan and van der Merwe 1991), and microbial community composition varies with age in other early successional systems (Nemergut et al. 2007). Therefore, the observed slow down in soil development may also correspond to an increase in the rate of decomposition as a fully functioning decomposer community establishes. More work is required to explore these ideas in detail.

What is particularly surprising about the curves for dry habitats is how much steeper and higher they are in comparison to other published data. While vegetation type plays a role in soil development through effects on productivity and litter biochemistry (Berendse 1998), and higher values of %LOI are reported for dunes of similar age under shrubs or forest (Gerlach et al. 1994; Salisbury 1925; Wilson 1960) this study specifically compared data from dune grasslands, and the Newborough data show much more rapid soil development than other studies. Climate and soil type also play a role. In temperate latitudes, soil development is usually faster under wetter conditions, while low soil pH leads to faster soil development (Wilson 1960). However, soil development rates in this study exceed both the acidic comparison sites (Blakeney – average rainfall 580 mm, and Studland – average rainfall 750 mm) and the site at Southport with a similar climate and sand mineralogy to Newborough (Ranwell 1959; Salisbury 1925)– average rainfall at both sites is 850 mm. One key difference is that most of the published data were reported in the 1920s. Therefore, the early successional soils will have been formed under different climate conditions and a different nitrogen deposition regime, a factor which has been alluded to by Berendse (1998) but not examined in detail until this study. It is also possible that the data describe 2 separate curves, and that the rapid increase in soil development will lead to a plateau higher than that observed for 140 year old soils whose initial formation occurred under different climate and nitrogen deposition regimes, although there is no way to test this hypothesis. Lastly, conditions specific to Newborough such as partial afforestation or management history may have contributed to the rapid soil development. However, a chronosequence for Merthyr Mawr, a non-afforested site in South Wales 200 km away, showed very similar rates of soil development over the same period (Jones et al. 2007). Therefore, it seems likely that factors operating over spatial scales of at least hundreds of kilometres, rather than site-specific conditions, have affected the rate of soil development.

A contrasting situation occurs in the wet dune habitats where organic matter accumulation is slower than in the published literature. However, these are not like-with-like comparisons. The studies from one dune area at Terschelling (Berendse et al. 1998; Lammerts et al. 1999) chart soil development after episodes of turf-stripping. This typically leaves a substrate containing residual organic matter, which at these Dutch sites is also partially de-calcified and speeds up subsequent soil development (Berendse et al. 1998). This contrasts with the development of embryonic dune slack vegetation on calcareous sand at Newborough and may explain the relatively faster soil development compared with Newborough.

The results suggest that large scale processes such as climate or pollution history have contributed to the rapid soil development observed here. This is backed up by the results of regression analysis in this study. Climate variables in the dry dunes explain up to 62 % of the variation in rates of soil development in combination. While these relationships are only statistical associations and may not be causal, nonetheless consistent patterns emerge, with faster soil development in the dry dunes associated with warmer temperatures and with drier summers, and negatively associated with summer storms. The positive link with autumn temperature and negative link with spring frosts suggest that a longer growing season may be one mechanism allowing a greater supply of organic matter to the system. Interestingly, it appears that drier summers promote soil development, perhaps implying that summer droughts do not inhibit plant productivity at this west coast UK site. Temperature should also increase rates of organic matter decomposition (McLachlan and van der Merwe 1991); but the net increase in soil development rates suggests that soil development in the dry dunes in this phase is controlled by plant productivity rather than organic matter decomposition. In the dune slacks temperature appears to play less of a role than in the dry dunes. Dune slack soil characteristics have been linked to hydrological regimes (Grootjans et al. 1998) and it is surprising that rainfall shows no significant associations with soil development in these wet habitats, given the controls that the water table has on rates of organic matter decomposition.

There is also a strong link of soil development with nitrogen deposition in the dry dunes. Nitrogen deposition at Newborough has increased by around 75 % since 1920, and this may partly explain the faster rates of soil development at Newborough compared with older studies. Experimental work at Newborough (Plassmann 2006) and in the Netherlands (ten Harkel et al. 1998) has shown that a proportion of excess nitrogen is retained in the system, and this would be expected to increase soil organic matter accumulation directly by promoting plant productivity. Phosphorus limitation is prevalent in calcareous dunes in The Netherlands where it limits the response of plant productivity to excess nitrogen (Kooijman and Besse 2002; Kooijman et al. 1998),, in which case nitrogen should play a lesser role in soil development. However, vegetation N:P ratios suggest that phosphorus limitation is not prominent at Newborough (Jones et al. 2004), while Plassmann (2006) suggests that phosphorus limitation in the older dune grasslands at Newborough may occur with a doubling of current levels of atmospheric nitrogen input. Therefore, nitrogen remains the main limiting nutrient at this site. However, nitrogen deposition and temperature are highly co-correlated, and it is not possible to separate their effects on soil development in this study. Rising atmospheric CO_2 concentrations increase N and C accumulation rates (Luo et al. 2006) and this may be another cause of faster soil development, but will also be co-correlated with average temperature and nitrogen deposition.

Sand dunes are dynamic systems and disturbance is a key factor which acts to hinder soil development. Average windspeed, Talbot's Mobility Index (Talbot 1984), and factors such as sand movement and salt spray, linked to distance to the sea all represent some form of disturbance and will impede soil development. However, summer gales was the only variable linked to disturbance which significantly explained any variation. The negative link with summer gales in the dry dunes suggests that it is extreme events such as storms rather than average climate conditions which cause the most disturbance. Ranwell (1958) reported maximum sand movement at Newborough occurring over the summer and autumn months, with one gale in May causing more sand movement than 3 preceding months of moderate weather.

Other location-specific variables like soil pH show surprisingly little effect on soil development. However, even the oldest dry dune soils at Newborough are not or hardly de-calcified, while in the dune slacks the lowest pH (water) is 5.8, so gradients in soil pH are fairly small. Slope angle also appears to have little effect on soil development, although micro-climate and rainfall infiltration are influenced by slope steepness. Frederiksen et al. (2006) explained variation in vegetation communities by comparison with distance from the sea and a suite of micro-climate and topographical indices. They found a strong effect of distance from sea, linked to successional age, on both vegetation communities and some soil parameters but, as in this study, found relatively little influence of micro-climate or topographical factors on vegetation and soils.

In this study, a high proportion of the variation in rates of soil development is explained in the dry dunes, up to 68.4 %, but a lower proportion of the variation (27.5 %) in the wet dune habitats. The relatively small sample size for the regression analysis of dry dune habitats should be noted, which increases the chance of artefacts in the results. Of the unexplained variation, part must be attributable to errors in ageing soil locations and to natural variability in soil development. However, variation may also be due to factors such as disturbance which this study has only indirectly been able to address, or factors causing local heterogeneity in soil development such as grazers (Salisbury 1952), and variations in vegetation type (Berendse 1998). These factors operating over longer periods of time, together with stochastic factors such as disturbance may help explain the variability in %LOI in the oldest dated soils. In the dune slacks where the environmental variables explained a much lower proportion of the variation, it is possible that other factors such as groundwater chemistry and hydrological regimes (Grootjans et al. 1998) play a role, as these can show considerable spatial variation even within a site (Jones et al. 2006; Stuyfzand 1993).

It is evident from the N accumulation rates of 16 – 67 kg N ha^{-1} yr^{-1} that, over the steepest parts of the curve, N accumulation greatly exceeds retention of atmospheric nitrogen deposition. Given atmospheric inputs of up to 10 kg N ha^{-1} yr^{-1} and a conservative assumption of 30 % retention of atmospheric N inputs based on leaching studies (Jones et al. 2005; ten Harkel et al. 1998), this would give retention of between 2 and 3.5 kg N ha^{-1} yr^{-1} of atmospherically derived nitrogen over the period of soil development. Therefore, atmospheric N deposition can only be one source of N entering the system and biological fixation is likely to also be a major source of N during this phase of soil development. N fixation may be via legumes, cyanobacteria or other N-fixing species such as the shrub *Hippophae rhamnoides*. Three stands of *H. rhamnoides,* approximately 10 m across had established at Newborough from seed, but were cleared in the 1990s. Soil sampling avoided any areas close to shrubs and cleared areas, therefore these stands are unlikely to influence the data. Survey data show that legumes reach a maximum 11 % cover at Newborough (Jones et al. 2002), and legumes could be a minor source of fixed N. However, cyanobacteria in sand are likely to be the major source of N fixation (Kumler 1997) and were estimated to fix 25 kg N ha^{-1} yr^{-1} in dune grassland at an East coast UK site, Blakeney Point (Stewart 1967). Such facilitation by nitrogen-fixers is an established part of ecological succession theory (Crocker and Major 1955). A conservative estimate of total biological fixation in this system must at least be equivalent to 10 – 60 kg N ha^{-1} yr^{-1}, assuming that other loss pathways of N such as denitrification are minimal. These data represent only the N pool in the soil which is typically 80 % of the total ecosystem N pool including N in above and below ground vegetation in established UK dune grasslands (Jones et al. 2002; Jones et al. 2005), therefore soil nitrogen accumulation rates at Newborough are slightly higher than total ecosystem N accumulation rates of 40 – 46 kg N ha^{-1} yr^{-1} in a 76-year chronosequence at Terschelling (Berendse et al. 1998) and higher than rates reported for heathland and an inland dune chronosequence in the Netherlands (Berendse 1998). Indeed, these rates are higher than any reported for comparable systems, although the soils here are very young and Knops and Tilman (2000) suggest that N accumulation rates decline with increasing N pools, which is supported by older dune chronosequences with average rates of ca. 4 kg N ha^{-1} yr^{-1} over 1000 years (Olson 1958b; Syers et al. 1970) and 1 kg N $ha^{-1}yr^{-1}$ over 10,000 years (Syers et al. 1970).

In summary, the detailed chronology for the first 140 years of dune soil development presented in this study shows a strongly non-linear pattern, with rates far exceeding those for other dry dunes in the literature. Regression analysis suggests that there are strong associations with factors operating on a broad-scale such as climate and nitrogen deposition, and that location-specific factors operating on a smaller scale are less important at this calcareous site where soils have not yet decalcified. Therefore, recent climate and/or nitrogen deposition regimes may have accelerated soil development compared with past rates. Nitrogen accumulation rates are high, and the data suggest that N inputs from biological fixation are roughly four times greater than from atmospheric deposition. The period of most rapid soil development commences more or less when full vegetation cover is established, and this has implications for site management, with particular importance attached to maintaining the open status of semi-fixed habitats in order to protect the obligate dune species which depend on them.

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Table 1. Relationships of broad-scale (climate, nitrogen deposition) and location-specific (soil pH, distance to sea, slope angle) variables with rates of organic matter accumulation in dry and wet dune habitats. Climate variables are also broken down by season (Win6 = Winter 6-months season; Spr3 = Spring 3-months season etc.). Significant variables are shown in bold.

	Dry habitats					Wet habitats				
	N	R^2	coeff	F	p	N	R^2	coeff	F	p
AveTemp	14	**45.2**	**0.1485**	**9.88**	**0.008**	40	8.8	0.0795	3.65	0.064
AveTemp_Win6	14	**37.7**	**0.1460**	**7.27**	**0.019**	40	**10.6**	**0.1095**	**4.5**	**0.041**
AveTemp_Sum6	14	**47.1**	**0.1306**	**10.68**	**0.007**	40	7.4	0.0618	3.03	0.090
AveTemp_Win3	14	26.6	0.1320	4.34	0.059	40	**11.9**	**0.1103**	**5.15**	**0.029**
AveTemp_Aut3	14	**48.8**	**0.1672**	**11.46**	**0.005**	40	8.1	0.0846	3.35	0.075
AveTemp_Sum3	14	26	0.1171	4.21	0.063	40	6.8	0.0708	2.79	0.103
AveTemp_Spr3	14	**42.7**	**0.0841**	**8.95**	**0.011**	40	6.8	0.0491	2.75	0.105
MaxTemp	14	**42.2**	**0.1191**	**8.75**	**0.012**	40	**10.5**	**0.0772**	**4.44**	**0.042**
MaxTemp_Win6	14	**33.3**	**0.0839**	**5.99**	**0.031**	40	**11.1**	**0.0794**	**4.75**	**0.036**
MaxTemp_Sum6	14	**48**	**0.1466**	**11.09**	**0.006**	40	9.6	0.0794	4.02	0.052
MaxTemp_Win3	14	**34.7**	**0.0861**	**6.38**	**0.027**	40	**11.8**	**0.0794**	**5.1**	**0.030**
MaxTemp_Aut3	14	**39.1**	**0.0944**	**39.1**	**0.017**	40	8.9	0.0613	3.7	0.062
MaxTemp_Sum3	14	**45.8**	**0.1746**	**10.16**	**0.008**	40	**10.1**	**0.0841**	**4.25**	**0.046**
MaxTemp_Spr3	14	**32.8**	**0.1025**	**5.85**	**0.032**	40	8.7	0.0783	3.61	0.065
MinTemp	14	**42.1**	**0.0836**	**8.73**	**0.012**	40	9.3	0.0529	3.9	0.055
MinTemp_Win6	14	**38.3**	**0.0590**	**7.44**	**0.018**	40	9.5	0.0547	4	0.053
MinTemp_Sum6	14	**46**	**0.1171**	**10.21**	**0.008**	40	8.4	0.0518	3.49	0.069
MinTemp_Win3	14	**37.3**	**0.0687**	**7.14**	**0.020**	40	**11.2**	**0.0627**	**4.8**	**0.035**
MinTemp_Aut3	14	**37.7**	**0.0626**	**7.26**	**0.020**	40	7.9	0.0418	3.28	0.078
MinTemp_Sum3	14	**45.8**	**0.1199**	**10.14**	**0.008**	40	9.3	0.0560	3.9	0.055
MinTemp_Spr3	14	**46**	**0.0887**	**10.2**	**0.008**	40	6.9	0.0458	2.82	0.101
Frost	14	**33.3**	**-0.0095**	**5.98**	**0.031**	40	**10.9**	**-0.0079**	**4.67**	**0.037**
Frost_Win6	14	**33.8**	**-0.0096**	**6.13**	**0.029**	40	**11.3**	**-0.0085**	**4.84**	**0.034**
Frost_Sum6	14	**37.3**	**-0.1929**	**7.14**	**0.020**	40	5.7	-0.0921	2.31	0.137
Frost_Win3	14	25.7	-0.0131	4.15	0.064	40	**14.4**	**-0.0129**	**6.38**	**0.016**
Frost_Aut3	14	**30.6**	**-0.0432**	**5.28**	**0.040**	40	6.9	-0.0324	2.8	0.102
Frost_Spr3	14	**43.9**	**-0.0412**	**9.41**	**0.010**	40	0.4	-0.0064	0.15	0.702
Rain	14	6.6	-0.0007	0.85	0.374	40	3.2	-0.0008	1.26	0.269
Rain_Win6	14	7.5	0.0024	0.97	0.345	40	2.8	-0.0015	1.09	0.304
Rain_Sum6	14	**29.8**	**-0.0016**	**5.1**	**0.043**	40	3.1	-0.0007	1.22	0.277
Rain_Win3	14	2.3	0.0007	0.28	0.607	40	0.6	-0.0007	0.21	0.647
Rain_Aut3	14	11	0.0012	1.48	0.247	40	1.8	0.0005	0.68	0.415
Rain_Sum3	14	17.8	-0.0018	2.59	0.133	40	5.5	-0.0012	2.2	0.146
Rain_Spr3	14	14.4	-0.0018	2.02	0.181	40	8.7	-0.0039	3.61	0.065
Gales	14	8.5	-0.0065	1.12	0.311	40	**12.4**	**-0.0089**	**5.36**	**0.026**
Gales_Win6	14	3.8	0.0044	0.47	0.505	40	**10.3**	**-0.0100**	**4.35**	**0.044**
Gales_Sum6	14	**29.8**	**-0.0164**	**5.09**	**0.044**	40	**10.8**	**-0.0232**	**4.58**	**0.039**
Gales_Win3	14	22.1	0.0107	3.4	0.090	40	0.2	0.0051	0.09	0.772
Gales_Aut3	14	11.7	-0.0128	1.58	0.232	40	**12.3**	**-0.0157**	**5.34**	**0.026**
Gales_Sum3	14	26.1	-0.0348	4.23	0.062	40	8.4	-0.0387	3.48	0.070
Gales_Spr3	14	26.8	-0.0244	4.39	0.058	40	**14.3**	**-0.0324**	**6.35**	**0.016**
Wind_speed	14	7.7	-0.0092	1	0.337	40	8.6	-0.0078	3.58	0.066
Mobility Index (Mo)	14	6.2	-0.4826	0.79	0.392	40	2.5	-0.3963	0.96	0.332
Nitrogen deposition	14	**42**	**0.0391**	**8.71**	**0.012**	40	2.2	0.0124	0.87	0.357
pH_water	9	28.8	0.0195	2.83	0.137	19	9.2	-0.0184	1.72	0.207
pH_$CaCl_2$	13	21	0.0153	2.92	0.115	19	2.8	-0.0174	0.49	0.494
Distance to sea	14	0.1	0.0000	0.01	0.929	40	1.4	0.0000	0.53	0.471
Slope (degrees)	9	19.3	0.0027	1.68	0.236					

Figure 1. Age of soil since locations were first vegetated plotted against %Loss On Ignition for a) dry dune and b) wet dune habitats.) Circles show locations where start date was known (i.e. since 1945), with white circles indicating locations not achieving 100 % vegetation cover at time of soil sampling; Triangles show locations where start date was unknown but for which the date at which they became fully fixed was known – here the minimum age is plotted; Squares show samples which were fixed prior to 1945 – ages are estimated based on maps and OSL dating. Equal error bars left and right of a data point show the likely age range. Unequal error bars denote uncertainty where only minimum or maximum age is unknown.

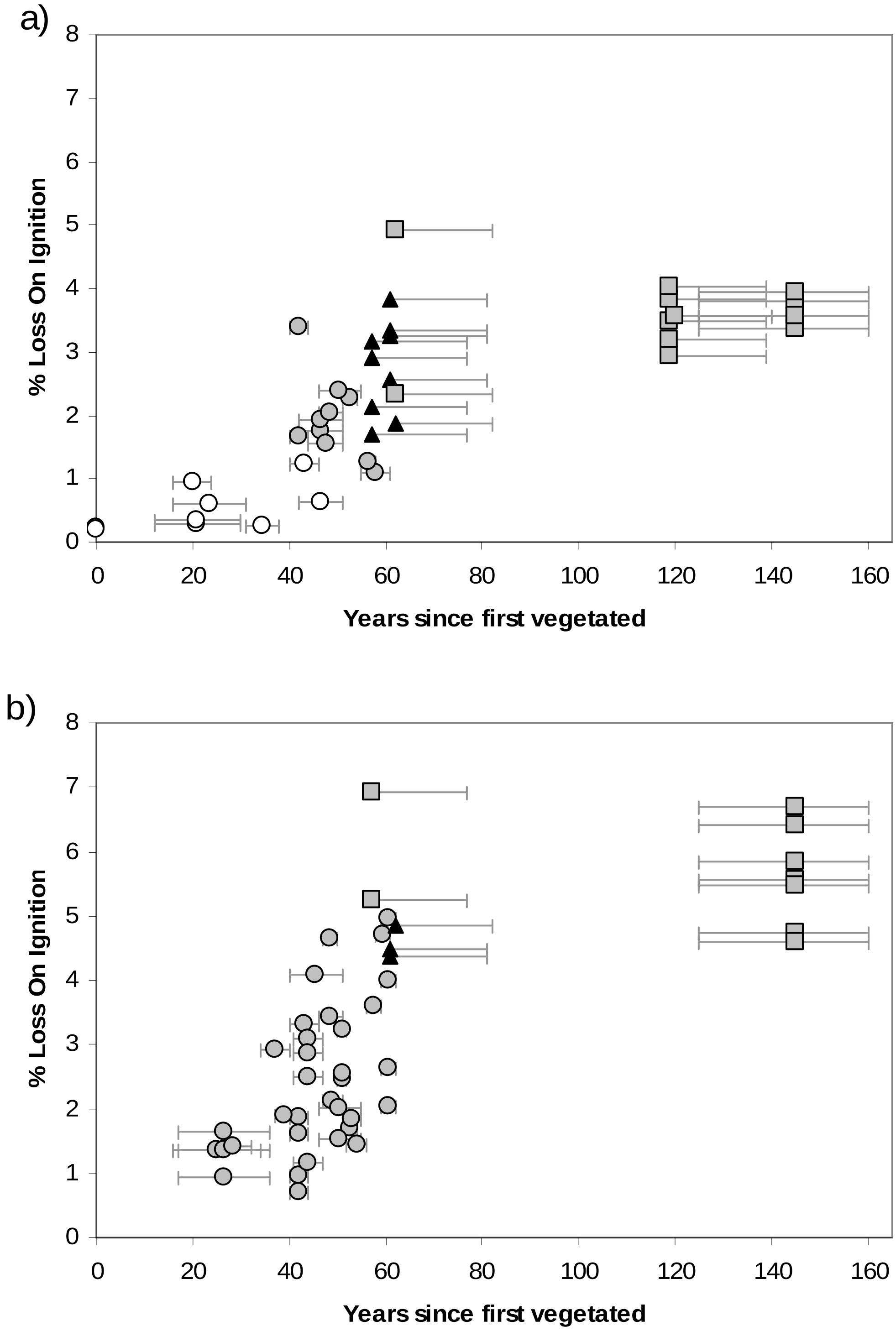

Figure 2. Comparison of Newborough %Loss On Ignition data from dry dune grasslands with those in the literature. Data from: South Haven (Wilson 1960), Southport and Blakeney (Salisbury 1922; 1925).

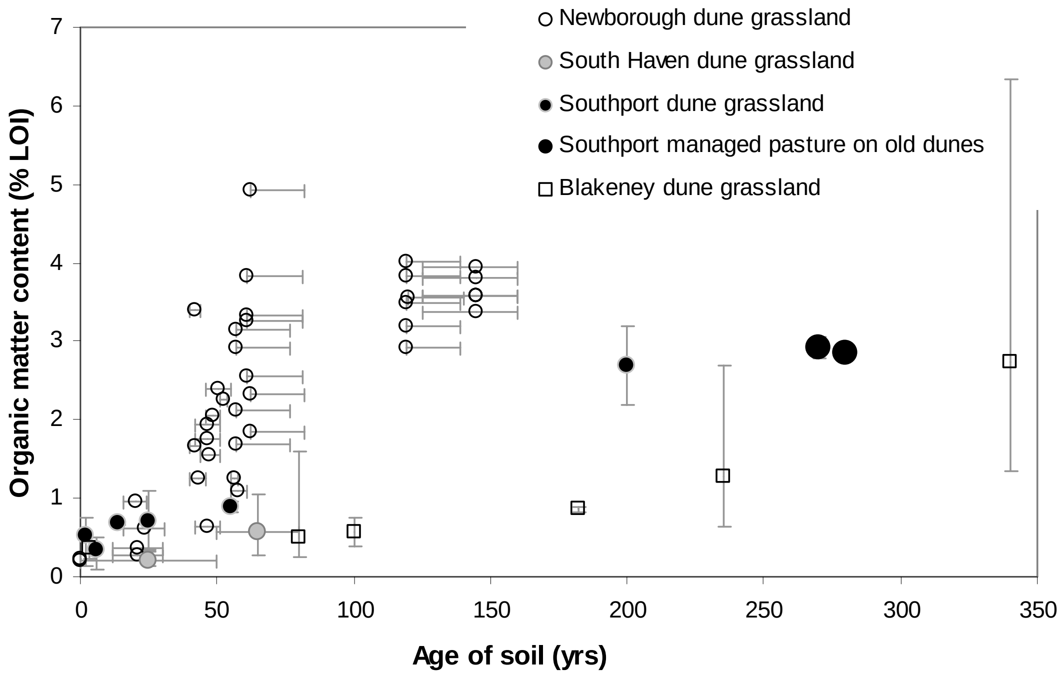

Figure 3. Comparison of Newborough data from dune slacks converted to organic matter pools (kg OM ha^{-1}), with those in the literature. Data from Terschelling from Berendse et al. (1998) – combined data from LFH and mineral sand to 20 cm, and Lammerts et al. (1999) – combined data from litter, humic and mineral horizons to 15 cm, but to 20 cm in the 80 year stage.

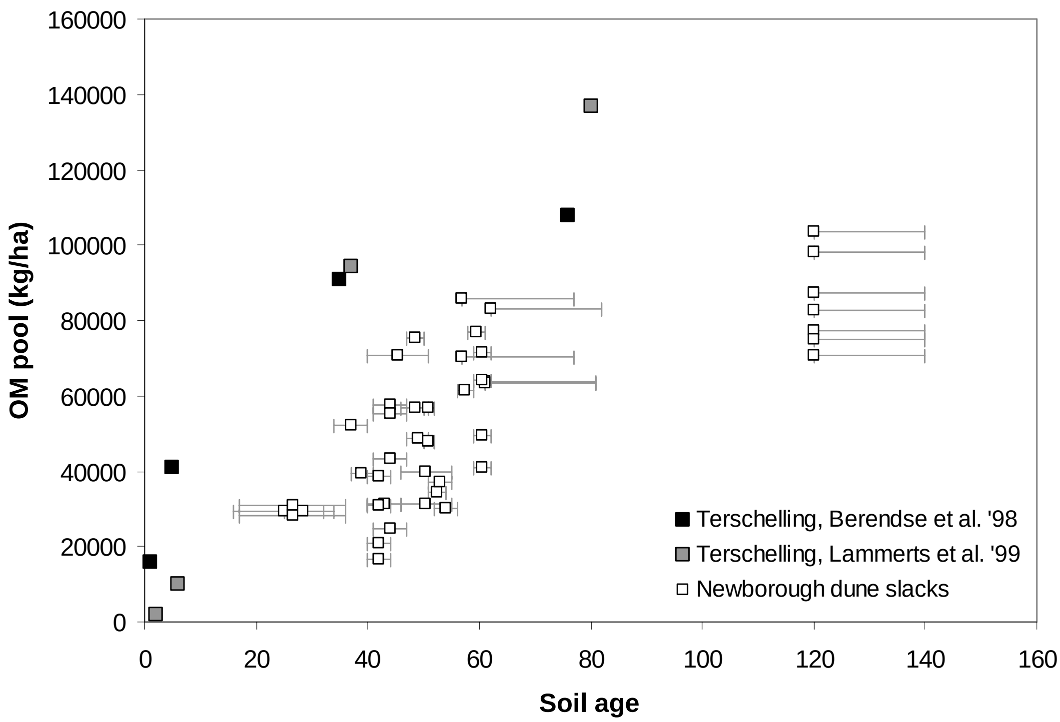

Figure 4. Summary of climate trends at Newborough since 1941 showing a) Average temperature, rainfall and reconstructed nitrogen deposition; b) Total rainfall broken down by 3-month seasons; and c) Number of days with gale force winds, broken down by 3-month seasons.

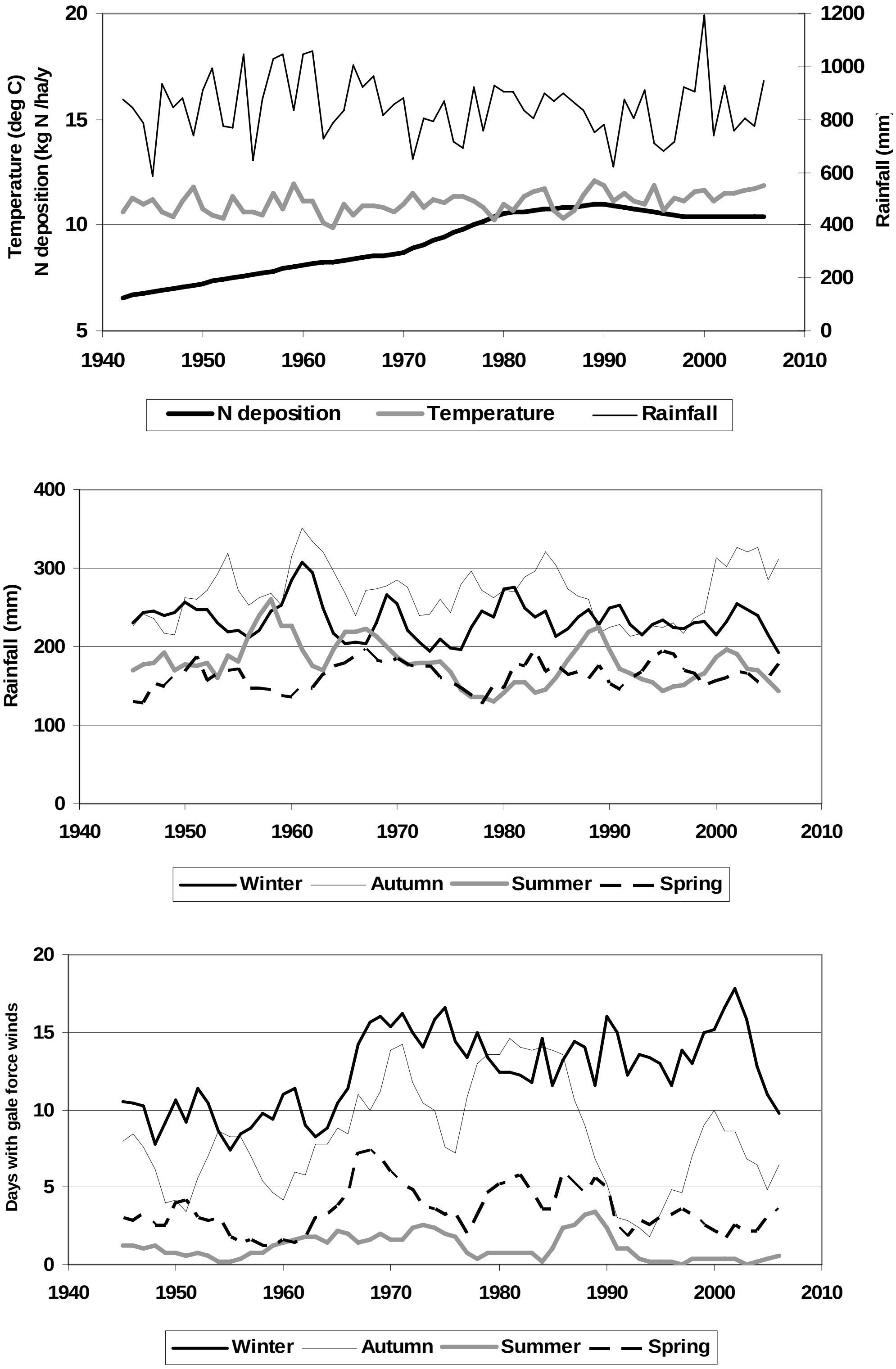

Figure 5. Principal components analysis showing inter-relationships between the climate and N deposition variables used in the regression analysis. Variable abbreviations as in Table 1.

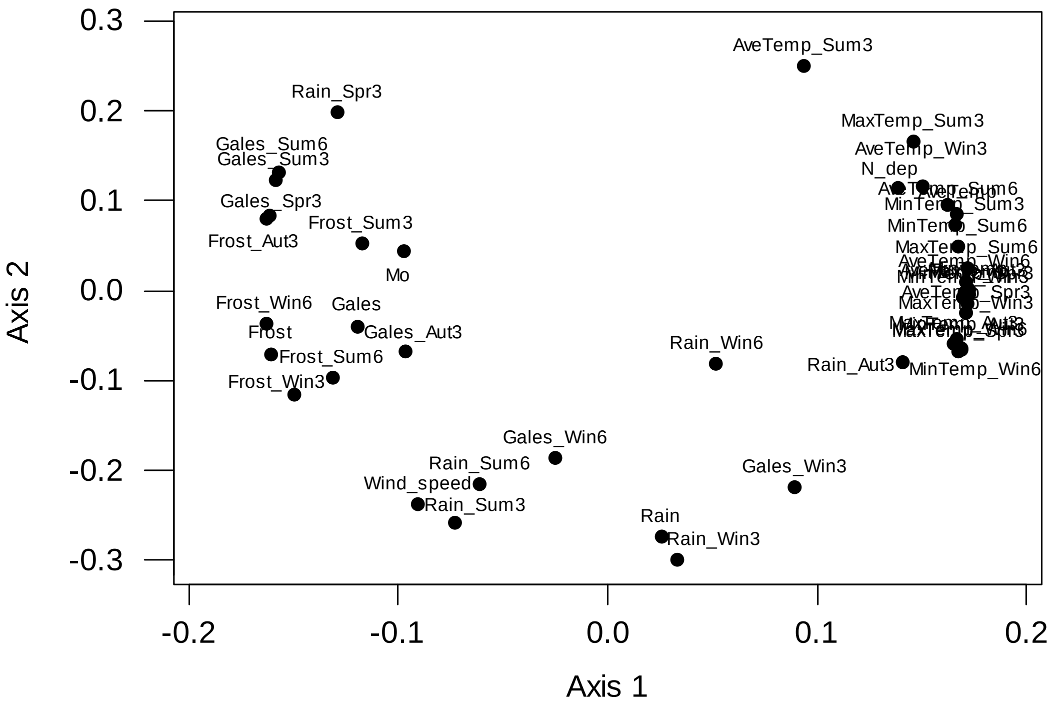

Figure 6. %LOI accumulation rates (%LOI yr^{-1}) plotted against soil age for dry (black points) and wet (white squares) dune habitats.

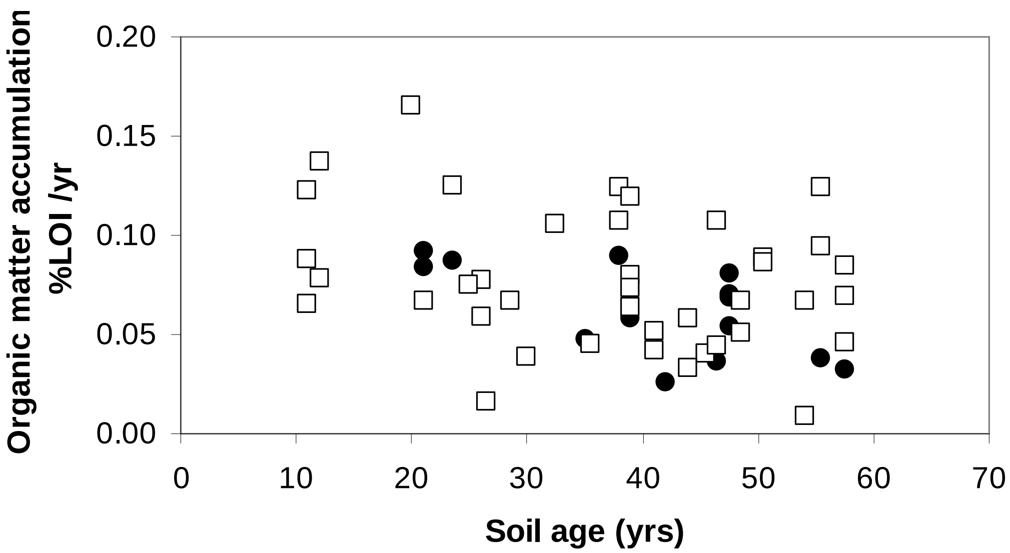

Figure 7. Nitrogen accumulation rates (kg N ha^{-1} yr^{-1}) plotted against soil age for dry (black points) and wet (white squares) dune habitats.