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Does atmospheric nitrogen deposition lead to greater nitrogen and carbon accumulation in coastal sand dunes?



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ABSTRACT

Atmospheric nitrogen (N) deposition is thought to accelerate ecological succession, causing a loss of diversity in species-rich dune grasslands and hampering restoration goals. We tested whether elevated atmospheric N deposition results in faster accumulation of soil C and soil N, using three high-resolution chronosequences of up to 162 years in coastal sand dunes with contrasting N deposition and soil base status (high N deposition calcareous and acidic dunes in Luchterduinen, the Netherlands (LD) and low N deposition calcareous dunes in Newborough, UK (NB)). We also used the process model CENTURY to evaluate the relative contribution of N deposition, climate, and soil pH. In contrast to our hypothesis we found that accumulation of soil C and N was greatest at the low N deposition site NB. Model simulations indicated a negative interaction between high N deposition and symbiotic N₂ fixation. From this we conclude that high N deposition suppresses and replaces N₂ fixation as a key N source. High N deposition led to lower soil C:N only in the early stages of succession (<20 years). The data also revealed accelerated acidification at high N deposition, which is a major concern for restoration of dune grasslands. More data are needed from acidic dunes from low N deposition areas to assess pH effects on soil C and N pools. Therefore, while N accumulation in soils may not be an issue, both acidification and plant community change due to elevated availability of mineral N remain major conservation problems. Restoration in degraded dune grasslands should focus on maintaining habitat suitability, rather than N removal from soil pools.

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1. Introduction

In coastal dune ecosystems, the accumulation of soil organic matter (SOM) during primary and secondary succession is a fundamental driver in the development of fixed dune grasslands (Olff et al., 1993; Ranwell, 1972; Van der Meulen and Jungerius, 1989). In the early stages of succession, sandy soils are low in SOM and have a small nitrogen (N) pool, so the availability of mineral N and water can limit plant productivity (Bartholomeus et al., 2012; Bohnert and Jensen, 1996; Johnsen et al., 2014; Tilman et al., 1996). Therefore, it has been suggested that a higher input of mineral N from atmospheric N deposition for several decades will accelerate succession of dune ecosystems by enhancing biomass production and litter input (Jones et al., 2004; Remke et al., 2009a, 2009b; Veer and Kooijman, 1997), leading to increased soil carbon and N stocks (Jones et al., 2008, 2013). The enhanced accumulation of soil C and N may hamper conservation and restoration of low

productive dune grasslands with a high biodiversity, even after atmospheric N deposition has reduced to low levels.

The mechanisms by which atmospheric N deposition may alter soil processes are both direct and indirect. Evidence from some experiments and from gradient studies suggests that extra N boosts plant productivity and plant tissue N content (Jones et al., 2004; Plassmann et al., 2009; Remke et al., 2009a, 2009b; Van den Berg et al., 2005), although these effects are not always observed in the field (Ford et al., 2016; Ten Harkel and Van der Meulen, 1996). The increased plant productivity enhances litter input, which accelerates accumulation of soil C and N. Accumulation of N in the soil may also be affected by changes in C:N ratio of the humic layer. C:N ratio is important because it controls many soil processes, with faster mineralisation as C:N falls below certain thresholds (Rowe et al., 2006). High N deposition may lead to increased plant tissue-N content and therefore a decreased C:N ratio in soil (Mulder et al., 2013; Remke et al., 2009b; Sardans and Penuelas, 2012). However, a gradient study in fixed dune grasslands suggests that a contrasting outcome for soil C:N ratios is also possible, where increased biomass production due to N deposition can actually increase C:N ratios by priming the system with carbon-

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rich biomass (Jones et al., 2004). The direct and indirect effects of N deposition may lead to higher N mineralisation, creating even more available N to fuel faster plant growth (Berendse, 1998; Sparrius et al., 2012). At the same time, high N deposition, high N mineralisation, and a low soil C:N ratio may also increase leaching losses (Phoenix et al., 2003; Rowe et al., 2006).

Accumulation rates of C and N in the soil are also influenced by natural factors. Soil pH may exert a major influence on organic matter accumulation since it controls decomposition rates. In addition, nitrification rates are also pH sensitive (Kemmitt et al., 2006), causing interactive effects of pH on N dynamics in the soil. Soil pH also governs phosphorus availability which together with N is usually the key limiting nutrient in dunes (Kooijman and Besse, 2002; Kooijman et al., 2016). Moreover, soil pH declines during succession because of soil organic matter accumulation, and decalcification. A high atmospheric N deposition also enhances acidification, due to elevated input of reduced N (NH_x), which produces protons when it is nitrified in the soil (Van Breemen et al., 1984). Thus, effects of elevated N deposition may differ between calcareous and acidic dunes and between different successional stages.

A main natural source of N is biological N_2 fixation by symbiotic and by free-living non-symbiotic bacteria. In dunes, rates of N_2 fixation from these natural sources can be high when *Hippophae rhamnoides* is present; it can fix 0.05–0.45 kg N ha^{-2} per day (Hassouna and Wareing, 1964; Kumler, 1997; Stewart and Pearson, 1967; Stuyfzand, 1993), which is equivalent to 9.1–82.1 kg N ha^{-2} yr^{-1} if N_2 fixation takes place during 50% of the year. In temperate grasslands symbiotic N_2 fixation ranges 0.1–10 kg N ha^{-2} yr^{-1} , and non-symbiotic N_2 fixation 0.1–21 kg N ha^{-2} yr^{-1} (Reed et al., 2011). Non-symbiotic N fixation may be hampered by high amount of available N relative to available P (Eisele et al., 1989), indicating negative effects of N deposition on non-symbiotic N fixation. Furthermore, symbiotic N fixing plants are more abundant in calcareous dunes than in acidic dunes (Weeda et al., 1987). This means that contribution of N fixation on soil N accumulation may differ between calcareous and acidic dunes and under high and low N deposition.

A major challenge in studying these multiple effects of N deposition on soil C and N accumulation is that soil development is a slow process, resulting from minor shifts in the balance between production and decomposition of SOM. Most fertilization experiments in the field do not run for long enough to detect enhanced N or C pools in the soil (Ford et al., 2016; Remke, 2010). Even long-running experiments struggle to detect small changes in large soil pools, while gradient studies can be confounded to a greater or lesser extent by other co-occurring gradients. However, chronosequence studies provide a technique to infer changes in soil processes over longer time-scales (Knops and Tilman, 2000; Stevens and Walker, 1970), provided certain assumptions are met (Johnson and Miyanishi, 2008). In addition, process-based soil development models can be used to test the influence of driving factors over long time scales by varying climate, N deposition and soil conditions as inputs.

In this study, we used data from three robustly constructed chronosequences in two sites with different levels of N deposition. The site with low N deposition is located in Wales, and consists of calcareous dunes. The site with high N deposition is located in the Netherlands, and consists of both calcareous and acidic dunes. We tested differences between the three chronosequences in accumulation rates of soil C and soil N, soil C:N ratios, and soil pH, patterns of vegetation structure and plant species richness. We further simulated the soil development over a 75 year period using the CENTURY model (Metherell et al., 1993), to evaluate the potential effects of N deposition, climate, and biological N_2 fixation. The research questions were:

- (1) Do dunes under high N deposition have greater accumulation of soil C and soil N, and lower soil C:N ratios than those under low N deposition; and is this reflected in the pattern of vegetation succession?
- (2) What are the relative contributions of atmospheric N deposition, climate and N_2 fixation to C and N accumulation in calcareous and acidic dunes?

2. Materials and methods

2.1. Site description

This study uses three chronosequences constructed at two temperate coastal dune ecosystems in Europe: Newborough Warren (hereafter called NB) in North Wales, United Kingdom (53:08 N 4:21 W), and Luchterduinen (hereafter called LD) in the Netherlands (52:18 N, 4:30E). NB only consists of calcareous dunes with a CaCO_3 content of approximately 1.7% in the young stages and 0.5–0.7% in old dune grasslands in the top 15 cm. LD has chronosequences in both calcareous and acidic dunes. In the calcareous dunes succession starts at a CaCO_3 content of 1.2 to 2.2%, and ends up in old stages with a content of 0–1.7% in the top 15 cm. Here, decalcification depth of old grasslands has a range of 0–22 cm. In the acidic dunes succession starts at a CaCO_3 content of 0.3–1.2%. The top soil layer is decalcified ca. 10–20 years after the start of succession. Decalcification depth of old grasslands is typically deeper than 30 cm. NB and LD have broadly similar climatic conditions (annual precipitation: 850 mm in NB and 805 mm in LD, annual average temperature: 10.2 °C in NB and 9.7 °C in LD, for the period of 1931–2014), but there are some difference in the seasonal patterns (Appendix A). LD has been exposed to a high level of atmospheric N deposition in the last decades with a peak of ca. 30–37 kg N ha^{-1} yr^{-1} during 1970–1990, whereas atmospheric N deposition level in NB has not been as strongly elevated and remained within the range of ca. 5–10 kg N ha^{-1} yr^{-1} (Fig. A.6 in Appendix A).

The chronosequences were established using high resolution aerial photographs available at least since 1940s in NB (1947, 1951, 1966, 1971, 1982, 1990, 2006; Jones et al., 2008), and 1930s in LD (1938, 1958, 1968, 1979, 1990, 2001, 2006, 2011; Aggenbach et al., 2013). When a bare spot in an aerial photo becomes vegetated in the aerial photo of the subsequent year, we assumed that succession started on that spot at the average year between the two sequential aerial photos. The succession age of the spot was calculated as the period between the year of succession started and the year of soil sampling (i.e. 2012). The age of the spots which were already vegetated in the oldest aerial photos were estimated with aid of additional historical records. In NB age of oldest stage (162 year) was estimated from historical maps (Jones et al., 2008), and second oldest stage (61 year) estimated from reconstructed aeolian history (Jones et al., 2010). In LD the age of the oldest stage was set at 97 year based on general records of aeolian history. In total, we have selected 48 plots in NB all with calcareous topsoil (ranging from 0 to 162 years old at year 2012) and 110 plots in LD (ranging from 0 to 97 years old at year 2012). LD plots were split in calcareous ($N = 48$; referred as LD calcareous) and quickly decalcifying dunes ($N = 62$; referred as LD acidic). An overview of the plots is given in Table B.1 in Appendix B. All plots ranging from bare sand to dry dune grasslands are independent from the phreatic aquifer.

2.2. Soil sampling

For each plot, volumetric soil samples were taken from 0 cm to 15 cm depth in 2012 or 2013 for NB and in 2012 for LD. The soil samples were weighed to calculate bulk density and, after removing large roots, dried at 65 °C and machine-ground. Soil organic C and N were measured by combustion on a Carlo Erba CSN analyser, after acidification to remove carbonates. pH in topsoil (0–5 cm depth for LD, 0–6 cm depth for NB) was measured by extracting fresh soils with demineralised water with a ratio 1:2.5 (w/v).

2.3. Vegetation recording

In all plots of LD, bare sand cover and species composition of vascular plants, mosses and lichens were recorded in 1 m × 1 m plots during summer 2012. For NB, species composition and bare sand cover were recorded in 2 m × 2 m plots ($n = 21$) as part of an earlier

chronosequence study at the same site (Jones et al., 2008, 2010), which shared many locations with the plots used for soil sampling in 2012. Succession age of the vegetation plots ranged from 5 to 150 years. We used bare sand cover as a vegetation structure parameter, and we calculated total species number for each plot as a measure for biodiversity.

2.4. Statistical analysis

Changes in soil C pool, soil N pool, soil C:N ratio, and soil pH over successional age were fitted for each chronosequence separately. Following relationships in Jones et al. (2008) a 3-parameter logistic curve ($a1 / (1 + \exp((a2 - \text{age}) / a3))$) was fitted to the increase in C pools and N pools over time. An asymptotic curve ($a1 + (a2 - a1) * \exp(-\exp(a3) * \text{age})$) was fitted to both C:N ratio and pH as in both cases the data approach an asymptote. Parameter $a1$ is referred as 'asymptotic' value in both curves. Parameter $a3$ of the logistic curve is the age value at the inflection point of the curve (with a low value indicating a strong increase), and parameter $a2$ is the scale parameter on the input axis. For the asymptotic curve parameter $a2$ is the intercept and $a3$ the log rate. Testing of differences between pairs of curves and the curve parameters was then conducted in R. The R functions `SSasympt` and `SSlogis` were used to fit the curves, within the function `nlsList`. Significant differences of N deposition were evaluated by comparing NB and LD calcareous, and differences due to initial calcium carbonate content by comparing LD calcareous and LD acidic. Differences between curves for individual parameters were assessed as significant when these were higher than twice the standard error of the difference.

Changes in bare sand cover and total species number along successional age were also fitted for each chronosequence separately. For bare sand cover we used a logistic curve ($a1 + a2 * \exp(-\text{age} / a3)$). For total species number different regression models were selected: a logistic curve ($a1 / (1 + \exp((a2 - \text{age}) / a3))$) for NB and LD calcareous, and a 2-order polynomial curve for LD acidic. Testing of differences between curve pairs for bare sand cover was conducted in the same way described above. This testing was not conducted for total species number, because the vegetation plots differed in size for LD and NB, and for LD calcareous and LD acidic, the best fit was acquired with different regression models.

2.5. CENTURY model

To simulate development of soil and vegetation, we used the CENTURY model (Metherell et al., 1993). The CENTURY model is internationally used and well validated with empirical data for both agricultural and natural ecosystems across biomes (e.g. Kelly et al., 2000; Schimel, 1994). CENTURY dynamically simulates decomposition of soil organic matter and associated dynamics of soil C and N, growth of vegetation, and hydrology. See Appendix C for more details about the model specification and optimization procedure. We optimized three model parameter values, which control maximum plant production, nutrient uptake by plant, and decomposition rate, based on observation data of soil C, soil N, and plant biomass. All three optimized parameter are global (i.e. not site-specific) parameters, not facilitating responses to any local factors such as N deposition level or soil pH.

2.6. Site-specific model input data

We used historical records of N deposition level (wet plus dry, NH_x plus NO_y) of NB and LD (Fig. A.6 in Appendix A). For NB, the back-calculated national profile for UK was calibrated to Newborough (Jones et al., 2008). For LD, the national average of N deposition level in the Netherlands (CBS et al., 2015) was corrected for the local N deposition level of LD for the period after 1946, by using the proportion of the local over the national average in 2014 (Velders et al., 2015), i.e. 84%.

Monthly average values of precipitation, minimum and maximum temperature were taken from weather station RAF Valley for NB

(<8 km from the plots) and weather station De Bilt for LD. The weather data of De Bilt were corrected for LD by using the proportion of difference between the De Bilt and the closest weather station to LD, Valkenburg (<15 km from the plots) in the recent year records. For computation of potential evapotranspiration, we used a simplified Penman equation (Linacre, 1977), multiplied with 0.75 to convert from lake surface to vegetated surface.

We assumed that the asymbiotic N_2 fixation (i.e. N_2 fixation by free-living microorganisms) occurred at a constant rate both in NB and in LD. We used the median value of temperate unfertilized grasslands (Reed et al., 2011), $5.7 \text{ kg N ha}^{-2} \text{ yr}^{-1}$. The fixed N was added to the ammonium pool of mineral N in the topsoil. In the CENTURY model symbiotic N_2 fixation is assumed to occur when soil mineral N is not sufficient to satisfy the plant N demand, having taken into account all the other factors which limit plant growth (e.g. temperature, moisture). The N fixers fix N in newly assimilated biomass with a C:N ratio of 26.7 gC gN^{-1} . We set an extra parameter value to define the proportion of symbiotic N fixers, and parameterized it based on vegetation records of each area. This parameter controls how much fraction of the plant N demand, at maximum, can be fulfilled by symbiotic N_2 fixation. Since there was no clear temporal trend in the observed proportion of symbiotic N fixers during succession, we used average abundance (i.e. cover in percentage) of symbiotic N fixers from vegetation record values all through the succession period: 6% for NB ($N = 21$), 5.4% for calcareous dunes in LD ($N = 48$), and 0.14% for acidic dunes in LD ($N = 62$). Note that effects of soil acidity on process rates are not included in the CENTURY model. Therefore, difference in model input values between calcareous and acidic sites in LD is merely the proportion of symbiotic N fixers.

2.7. Model simulation and analysis of model outputs

Succession of soil and vegetation was simulated for the three chronosequences (NB calcareous, LD calcareous, and LD acidic) for 75 times each (i.e. 1-year-old dune to 75-year-old dune). Each simulation starts from bare soil (see Appendix C for model initial values). For model simulation of each age, we used different data series of N deposition and meteorology of the corresponding years (e.g. 1938–2012 for 75-year-old simulation, 1939–2012 for 74-year-old simulation, etc.). Plausibility of the model was tested by comparing the model output of soil C and N accumulation, soil C:N ratio, and above-ground plant productivity for the three chronosequences with their field observation data of multiple ages (see Appendix B for more details).

The scenarios with actual conditions as described above are hereafter referred to as 'actual scenario'. In order to disentangle the contribution of different factors on soil and vegetation succession, we ran extra scenarios for 75 years (from 1938 to 2012). First, for each of the three sites, the model was run with a low N deposition (hereafter referred to as 'lowN scenario'). For this, we used the N deposition level of 1900 in the Netherlands, i.e. $0.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Second, the model was run with absence of symbiotic N_2 fixation (hereafter referred to as 'noNfix scenario'). Third, we ran the model with the low N deposition level and no symbiotic N fixers (hereafter referred to as 'lowN + noNfix scenario'). Since the difference between sites in lowN + noNfix scenario is merely due to the meteorological conditions, this scenario can be considered as baseline scenario reflecting only the effect of climate. We consider the difference between the lowN + noNfix scenario and lowN scenario as the effect of symbiotic N_2 fixation; the difference between lowN + noNfix scenario and noNfix scenario as the effect of atmospheric N deposition; the difference between lowN + noNfix scenario and actual scenario as the combined effect of symbiotic N_2 fixation and atmospheric N deposition. When the combined effect of symbiotic N_2 fixation and atmospheric N deposition was larger or smaller than the sum of effects of symbiotic N fixation and atmospheric N deposition, we consider the interactive effects of these two factors as positive or negative, respectively.

3. Results

3.1. Observed soil C and N accumulation under low and high N deposition levels

For all chronosequences, regression models for C and N accumulation had a high r^2 and significant p -values for the regression parameters ($p < 0.001$) (Table 1). Soil C pool rose with increasing age and levelled off after around 60–80 years (Fig. 1) to a level of approximately 2.3 kg C m^{-2} in LD and 2.8 kg C m^{-2} in NB. Soil N also increased with age and levelled off to a level of 0.18 kg N m^{-2} in LD and 0.24 kg N m^{-2} in NB (Fig. 1). Difference in initial calcium carbonate content between acidic and calcareous dunes, only tested for LD, had no effect on the final C and N pool (curve asymptotes), and other regression parameters (Table 1). Unexpectedly, the final pools of C and N were significantly higher at the low N site in NB than at the high N calcareous site in LD ($p = 0.039$ for C pool, $p = 0.015$ for N pool). In NB, accumulation of soil N was much higher than the cumulative inputs from atmospheric N deposition (Fig. B.1.b in Appendix B). For example, N deposition accounted for only 26% of the N pool at the succession age 65 years. In LD cumulative N deposition was equivalent to 112 and 92% of the N pool at age 75 years respectively for the calcareous and acidic chronosequences.

3.2. Observed soil C:N ratio

For LD calcareous and LD acidic the asymptotic regression models of C:N ratio with age had a moderate r^2 , and low p -values for the model parameters ($p < 0.001$), while for NB r^2 was very low (Table 1). In NB, C:N ratio did not change over time. In both LD chronosequences, C:N ratio rose in the early stage (0–20 year) and then levelled off to approximately 13.5 (Fig. 1). Differences in N deposition had a significant effect ($p = 0.008$), leading to a lower intercept in LD calcareous compared to NB. The asymptotic values did not differ, which means that N deposition only affects the C:N ratio in the early stages (<20 years). For LD there was no clear effect of calcium carbonate content on C:N ratio ($p = 0.052$).

3.3. Observed topsoil pH

All chronosequence regression curves of pH on age had a high r^2 and significant p -values ($p < 0.001$) for all regression parameters (Table 1; Fig. 1). N deposition had no effect on intercept and asymptote, indicating that initial and final pH values were the same for NB and LD calcareous. However, N deposition strongly affected the log rate ($a3$),

indicating faster acidification in LD calcareous than in NB ($p < 0.001$). Acidification was also strongly affected by initial calcium carbonate content ($p < 0.001$), with the asymptotic values being much higher in LD calcareous than in LD acidic (5.8 and 4.0, respectively).

3.4. Bare sand cover and total plant species number

In all chronosequences, bare sand cover declined quickly when succession starts, and became low after 30 years (Fig. 2). The regression curves only differed for the asymptotic parameter between NB and LD calcareous. In LD calcareous, plots in the older stages still had some bare sand (0–30%), while in NB bare sand cover was very low (0–3%). For total species number (vascular plants, mosses, and lichens), both calcareous chronosequences follow the same pattern: a strong increase between 0 and 20 years, and at older age species richness stays constant (Fig. 2). The species number was higher in NB compared to LD calcareous, probably due to the larger plot size. The trend in LD acidic differed strongly from both calcareous chronosequences. Species richness increased in early succession stages, but declined again between the period 39–49 years and 97 years.

3.5. Model plausibility for predicting soil and vegetation succession

Model performance against observed data is shown in Fig. B.1 in Appendix B for C pool, N pool, C:N ratio, and above-ground vascular plant biomass. The model predicted soil C accumulation reasonably well. Soil N accumulation was underestimated, especially for NB and LD acidic. Soil C:N ratio was overestimated by the model, but the increase in soil C:N ratio in the beginning of succession, which was observed clearly in LD, was well reproduced by the model. The predicted above-ground plant production was in the same range for old stages of NB, lower for young stages of NB, and generally higher for LD.

3.6. Contribution of different N sources to soil N accumulation

The CENTURY model outputs reveal the contribution of different factors to N accumulation and their relative importance on soil development. After 75 years of succession, the effect of climate on N accumulation was similar between LD and NB (Fig. 3). In the two calcareous areas, there was a negative interactive effect of symbiotic N fixers and atmospheric N deposition, i.e. elevated N deposition switched off a part of the symbiotic N_2 fixation. In the calcareous dunes of NB, with low N deposition, the potential contribution of atmospheric N deposition to total N pools in the soil was relatively low, which suggests that most N came from symbiotic N fixers. In LD calcareous, where atmospheric N deposition level was high, the contribution of N deposition was higher than in NB. However, in LD calcareous, symbiotic N fixers also contributed strongly to N accumulation, but much of the excess N was lost from the system through leaching. In LD acidic, the contribution of atmospheric N deposition to soil N accumulation was very large in comparison to that of symbiotic N_2 fixation, because symbiotic N fixers were hardly present.

4. Discussion

4.1. Effects of elevated N deposition on accumulation of soil C and soil N

Our hypothesis was that a long period of N deposition speeds up the accumulation of soil N and C. However, the empirical data of accumulation of soil N and C in the calcareous chronosequences indicated the opposite, despite the 2.6 times higher cumulative atmospheric N deposition in LD than in NB over the past 75 years. The model outputs suggest that microbiological N_2 fixation was an important N source for ecosystem development at both sites, but with considerable excess N leached at the high N deposition site, consistent with observations in other studies (Stuyfzand, 1993; Ten Harkel et al., 1998). However, the model outputs suggested

Table 1

Statistics of the regression models of C pool, N pool, C:N ratio and pH of the topsoil on succession age for the chronosequences in Newborough (NB calcareous), Luchterduinen calcareous (LD calcareous) and Luchterduinen acidic (LD acidic). C pool and N pool were fitted with a logistic model: $a1 / (1 + \exp((a2 - \text{age}) / a3))$; C:N ratio and pH were fitted with an asymptotic model: $a1 + (a2 - a1) * \exp(-\exp(a3) * \text{age})$. P-values model parameters: * $P < 0.001$. Where significant, differences between chronosequences for each model parameter are indicated with letters.

| Variabels | Chronosequence | r^2 | $a1$ ave \pm SD | $a2$ ave \pm SD | $a3$ ave \pm SD |
|-----------|----------------|-------|-------------------------------|-----------------------------|-----------------------------|
| C pool | NB calcareous | 0.71 | 2.89 \pm 0.21 ^a | 31.9 \pm 4.4 [*] | 19.3 \pm 3.9 ^a |
| | LD calcareous | 0.81 | 2.28 \pm 0.11 ^b | 22.9 \pm 3.3 [*] | 10.3 \pm 2.2 ^b |
| | LD acidic | 0.70 | 2.29 \pm 0.13 ^b | 29.1 \pm 3.0 [*] | 13.5 \pm 2.9 ^b |
| N pool | NB calcareous | 0.68 | 0.24 \pm 0.02 ^a | 27.9 \pm 4.2 [*] | 16.4 \pm 3.7 [*] |
| | LD calcareous | 0.78 | 0.19 \pm 0.01 ^b | 25.6 \pm 4.4 [*] | 14.8 \pm 3.3 [*] |
| | LD acidic | 0.76 | 0.17 \pm 0.01 ^b | 29.3 \pm 3.0 [*] | 16.4 \pm 3.1 [*] |
| C:N ratio | NB calcareous | 0.06 | 13.16 \pm 6.83 | 10.7 \pm 0.6 ^a | -5.2 \pm 4.3 |
| | LD calcareous | 0.46 | 12.59 \pm 0.45 [*] | 7.4 \pm 0.8 ^b | -2.6 \pm 0.5 [*] |
| | LD acidic | 0.52 | 13.96 \pm 0.46 [*] | 6.5 \pm 0.9 ^b | -2.6 \pm 0.3 [*] |
| pH | NB calcareous | 0.62 | 5.19 \pm 0.79 ^{ab} | 7.9 \pm 0.2 ^a | -4.7 \pm 0.5 ^a |
| | LD calcareous | 0.63 | 5.77 \pm 0.24 ^a | 8.3 \pm 0.3 ^{ab} | -3.1 \pm 0.4 ^b |
| | LD acidic | 0.89 | 4.01 \pm 0.14 ^b | 8.6 \pm 0.2 ^b | -3.1 \pm 0.1 ^b |

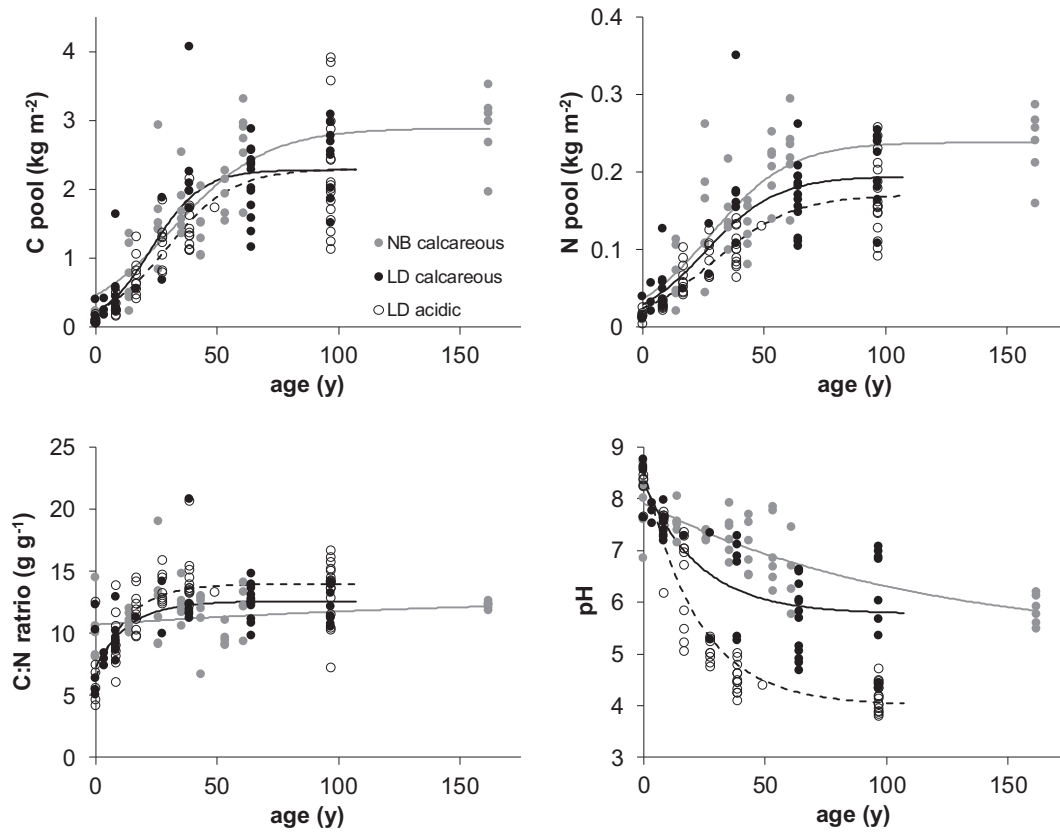


Fig. 1. Changes in topsoil C pool, N pool, C:N ratio and pH with succession age for Newborough (NB calcareous), acidic Luchterduinen (LD acidic), and calcareous Luchterduinen (LD calcareous). Lines are the regression models regressed by age (NB calcareous: grey; LD calcareous: black; LD acidic: dashed black).

that N₂ fixation was considerably lower at the high N deposition site, suggesting that N deposition switched off much of the symbiotic N₂ fixation. N₂ fixation can be switched off when mineral N in the soil is sufficient for demand (Tang et al., 1999), as shown by experiments with N-fixing species present such as *Hippophae rhamnoides* (Kato et al., 2007) and *Trifolium repens* (Macduff et al., 1996), as well as asymbiotic N₂ fixation in temperate grasslands (Keuter et al., 2014).

Higher N accumulation in NB might also be explained by the higher plant productivity, due to slightly lower drought stress in NB than LD. The model results suggested that differences in climate had little effect on the outcomes for soil C and N pools, because drought stress in LD simultaneously reduced both plant growth and decomposition of soil organic matter (Appendix A). However, the lower Ellenberg moisture values coupled with greater bare sand cover in LD, although only significant in older successional stages, suggested that drought stress may

exert a stronger negative effect on productivity in LD than NB. To access the effect of drought stress on N and C accumulation, more extensive analyses of soil moisture conditions are needed based on high frequency meteorological data and local soil moisture properties. Higher N accumulation in NB may also be associated with higher abundance of eutrophic species (as indicated by higher Ellenberg N values for NB than LD; results not shown), and might be linked to differences in geochemical properties of the dune sand between NB and LD.

A gradient study showed that high N deposition led to three times higher soil organic matter content in old acidic dunes, while there was no effect on calcareous dunes (Remke et al., 2009b). Therefore, acidic dunes may be more sensitive to enhanced N accumulation due to N deposition. However, we could not make the equivalent comparison for acidic dunes since we are not aware of any similar high resolution chronosequences spanning this age range at low N deposition sites.

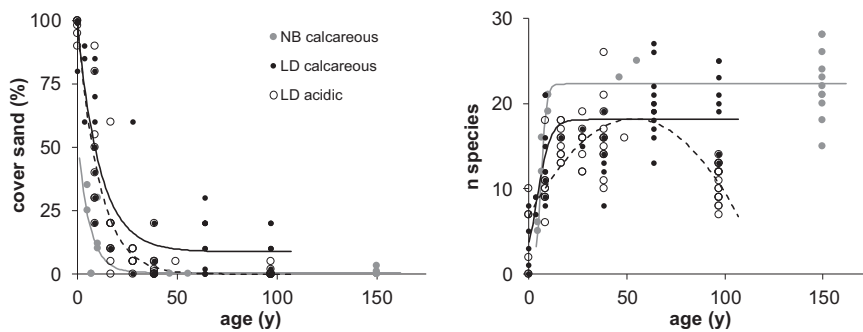


Fig. 2. Changes in bare sand cover and total species number (vascular plants, mosses, and lichens) with succession age for Newborough (NB calcareous), acidic Luchterduinen (LD acidic), and calcareous Luchterduinen (LD calcareous). Lines are the regression models regressed by age (NB calcareous: grey; LD calcareous: black; LD acidic: dashed black). Note the different sampling area for species richness: NB is species per 4 m², LD is species per 1 m².

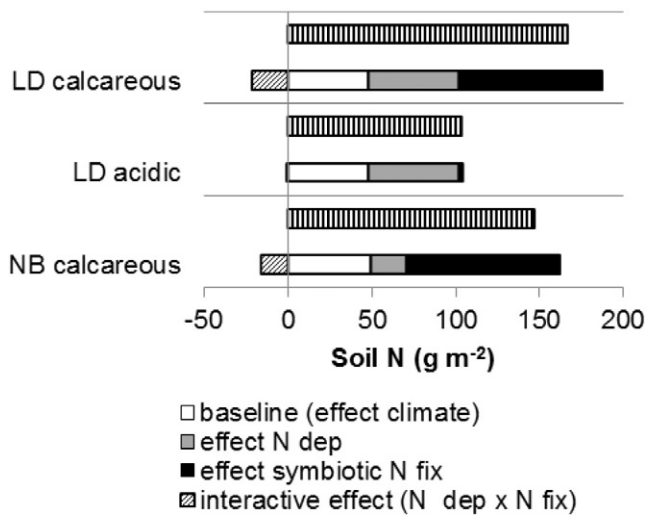


Fig. 3. CENTURY outputs for N pool in actual scenario and contributions of atmospheric N deposition, symbiotic N fixers, and climate to soil N pool after 75 years of simulation (from 1938 to 2012) for Newborough (NB calcareous), acidic Luchterduinen (LD acidic), and calcareous Luchterduinen (LD calcareous). See Section 2.7 for how contributions were calculated from a series of simulation scenarios.

4.2. Effect of elevated N deposition on soil C:N ratio

Our empirical data show an effect of atmospheric N deposition on the quality of organic matter (i.e. lower C:N ratios in high N deposition sites) in early successional stages. A direct effect of high N deposition would be an increased uptake of N by plants, and therefore a decrease of the C:N ratio of plant biomass and litter (Berendse, 1998; Remke et al., 2009b; Van den Berg et al., 2005). Also, high N deposition may, especially in young stages, stimulate growth of microorganisms that generally have lower C:N ratios than soil and plant litter (Cleveland and Liptzin, 2007). However, the lack of difference in C:N ratio in older stages remains unexplained, despite contrasting evidence for both lower (Remke et al., 2009b) and higher (Jones et al., 2004) C:N ratios observed in the field.

4.3. Model uncertainty

While our model was able to reproduce the overall patterns of long-term soil succession in dune grasslands, there were some mismatches between the model prediction and field observations. Firstly, symbiotic and asymbiotic N_2 fixation is one of the largest unknowns in the N inflow of ecosystems (Reed et al., 2011), yet their contribution to N and C accumulation could be significant (Pluis and De Winder, 1989). Sensitivity analysis showed that the modelled N accumulation was strongly affected by the parameters that control symbiotic and asymbiotic N_2 fixation (Appendix B). Thus, improved parameterization for N_2 fixation is a step to improve the model. Secondly, our model underestimated soil C and N accumulation for acidic sites. The only mechanism of pH effects included in our model is the higher amount of symbiotic N fixers in calcareous sites than acidic sites. However, pH potentially influences other processes too, such as plant productivity, SOM decomposition and N transformations, which would require additional site-specific measurements to adequately parameterise the model. Thirdly, we did not include grazing effects in the model due to lack of quantitative information about grazing intensity in the past, whereas our plots have been under different grazing regimes of cattle, sheep, and wild rabbits. Since grazing can have considerable effects on SOM accumulation in dune grasslands (Kooijman and Smit, 2001), improvement of the model performance relies on exact records of the grazing history for each plot.

4.4. Effects of N deposition on soil acidification and plant species diversity

Acidic dune grasslands are sensitive to accelerated decalcification and acidification of the topsoil due to atmospheric pollution because of the relatively low acid buffer capacity (Kooijman and Besse, 2002; Remke et al., 2009b; Stuyfzand, 1993). The acidic chronosequence in the high deposition area showed a fast drop of topsoil pH, which was much stronger than the trend of pH in chronosequences at Spiekeroog (Germany) and South Haven Peninsula (UK) with a comparable calcium carbonate content in the pioneer stage and with a relative low deposition (Gerlach et al., 1994; Wilson, 1960). Acidification affected the plant communities, with a drop in species richness in acidic grasslands when topsoil pH falls below 4.5–5.0, while in the calcareous grasslands species richness stayed constant, and topsoil pH remained high (5.5–7.0). This was reinforced by a decline in basiphilous species like *Viola curtisii*, *Cerastium semidecandrum* and an increase in acidophilous species like *Cladonia portentosa* and *Teesdalia nudicaulis*. The rapid acidification in the acidic dune grasslands due to N deposition therefore creates a legacy effect that will hamper restoration.

4.5. Implications for nature management

Our results indicate that high N deposition does not accelerate C and N accumulation in calcareous dunes due partly to suppression of N_2 fixation at high mineral N inputs, and also due to leaching of excess N as a result of the low retention capacity for N in dune soils. However, we cannot draw conclusions about accelerated accumulation rates in acidic dune grasslands due to lack of low N sites. Since soil N pools in calcareous Grey dunes are not increased by legacy effects of elevated N accumulation, then topsoil removal for this reason is not necessary. However, while N pools are not elevated, there is a wide literature documenting eutrophication effects in calcareous dunes such as declines in plant species richness (Field et al., 2014; Kooijman et al., 2017), possibly due to increased availability of soil mineral N (Jones et al., 2004). In addition, increased decalcification and acidification due to N deposition also reduces plant species biodiversity of dune grasslands. Restoration in dune grassland exposed to a high N (and legacy S) load should therefore focus on measures that maintain habitat suitability and restore a high base status of the topsoil (e.g. Jones et al., 2017). Soil restoration can be achieved by stimulating small-scale aeolian processes that create base-rich soils in deflation zones with renewed soil succession, and by deposition of calcareous sand in existing dune grasslands (Brunbjerg et al., 2014; Van Boxtel et al., 1997). Another measure is sod-cutting of superficially decalcified soils, which increases topsoil pH and favours basiphilous dune grassland species on a short time scale (Van Til and Kooijman, 2007). Remke et al. (2009b) found that the vegetation of old stage acidic dune grasslands is very sensitive to acidifying N deposition in a relatively low range (wet deposition 5–8 kg N ha⁻¹ yr⁻¹). Therefore, for old acidic dune grasslands, these measures are sustainable only when N load drops below this range.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2016.12.007>.

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