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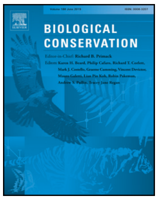

Does atmospheric nitrogen deposition lead to greater nitrogen and carbon accumulation in coastal sand dunes?

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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 N_2 fixation. From this we conclude that high N deposition suppresses and replaces N_2 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.

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

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