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Long-term changes in calcareous grassland vegetation in North-western Germany – No decline in species richness, but a shift in species composition

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ABSTRACT

We aimed to answer the question of whether the species richness and composition of calcareous grasslands in North-western Germany had changed over the last 70 years as a result of atmospheric nitrogen (N) deposition. In total, 1186 plots of *Festuco-Brometea* (alliance *Bromion erecti*) grasslands from the sub-oceanic regions of the country were compiled (1061 plots from literature sources spanning a time period from 1936 to 1996, 125 new plots from 2008). Environmental descriptors recorded for each plot included geographic coordinates, altitude, heat index (combining slope and aspect), mean Ellenberg indicator values for light, soil moisture, soil pH and soil N, and cumulative N deposition (the latter being highly positively correlated with the year of sampling).

In a Detrended Correspondence Analysis, the sample plot scores along axis one were highly correlated with the mean Ellenberg N-values, those along axis two were significantly affected by the year of sampling. In a general linear model, species richness of vascular plants showed a markedly hump-shaped relationship with mean Ellenberg N-value, whereas it was weakly affected by year (cumulative N load). Species with a significant negative trend over time were more often (than expected by chance) habitat specialists of dry grasslands, small, light-demanding and winter-green or evergreen with smaller seeds and scleromorphic leaves. In contrast to what has been found for acidic grasslands, N deposition in calcareous grasslands did not result in a decline in species richness, most likely because calcareous grasslands are water- and phosphorus-limited, and are well-buffered in terms of soil pH. To prevent a further change in species composition towards more mesophytic communities, grassland management by the site managers needs to be intensified.

1. Introduction

Atmospheric nitrogen (N) deposition and the subsequent eutrophication of terrestrial and aquatic ecosystems have been recognized as global processes where the planetary thresholds have already been overstepped (Rockström et al., 2009). In Central Europe the deposition of N exceeds 10–15 kg ha^{-1} year^{-1} in semi-natural vegetation and 20 kg ha^{-1} year^{-1} in coniferous forest, and the values are higher or even much higher in areas of intensive agriculture (Sutton et al., 2011). In Germany, the emission rates for nitrogen oxides have considerably decreased since 1990, whereas those for ammonium have been largely stable over the past years (http://www.umweltbundesamt.de/). In general, the emissions of N in Europe and other parts of the world are projected to increase during the next decades (e.g., Gruber and Galloway, 2008). The effects of N deposition on plant-species composition and richness have been documented for several vegetation types, based on three lines of evidence. First, experiments conducted in various habitat

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types have shown that N addition is often associated with an increase in biomass and a simultaneous decrease in species richness (Bobbink et al., 2010). In a recent meta-analysis, however, De Schrijver et al. (2011) showed that these effects on plant biomass and richness are vegetation type-dependent and that species of different life forms are differently affected. A second source of evidence relies on descriptive comparisons of areas situated along a geographic gradient in N deposition, for example in North European forests (Diekmann et al., 1999) and in British grasslands and heathlands (Stevens et al., 2004, 2006; Maskell et al., 2010). These spatial studies have largely supported the experimental results, showing a general decline in species richness, a decrease in species indicative of nutrient-poor sites, and a shift in functional types from forbs to grasses. The third way to examine effects of atmospheric pollution is a temporal approach, comparing plots sampled at a time with low N deposition with more recent plots having been exposed to higher deposition levels. Such time-series analyses have mainly been conducted in forests based on the monitoring of permanent plots (e.g., Diekmann et al., 1999), but have also been applied using a non-permanent design (Diekmann and Duprè, 1997; Gaudnik et al., 2011). Provided that the number of plots is large and that the data set is not spatially or temporally biased, this approach has some advantages compared to a permanent plot design in that it can be more representative through covering larger regions and more plots.

Eutrophication-driven changes in European vegetation are particularly well studied in acidic grasslands, which have suffered from a steep decline in species richness mainly caused by an increase in a few competitive grasses at the expense of forbs and dwarf shrubs (Stevens et al., 2006, 2011a; Duprè et al., 2010; Maskell et al., 2010). These temporal trends coincide closely with the results of N-addition experiments in grasslands (see De Schrijver et al., 2011). Surprisingly, the effects of N deposition in calcareous grasslands are less well documented, although these grasslands are among the most species-rich habitat types in Europe and of focal interest to nature conservationists across the continent. In one of the few long-term studies from Britain, Bennie et al. (2006) re-surveyed 92 plots from English chalk grasslands that were first surveyed in 1952–53. They showed a decline in species richness, a decrease in species associated with inherently infertile conditions and an increase in species typical of more mesotrophic grasslands, thereby indicating an effect of nutrient enrichment. In contrast, an increase in α diversity over 70 years was observed in a re-survey of 88 calcareous grassland sites in the English county of Dorset (Newton et al., 2012). In another permanent plot study from southern Germany, revealing similar results, the vegetation changes were attributed mainly to a change in management, namely a decrease in grazing intensity (Hagen, 1996). Again, these changes and their interpretation coincide with results from various N-addition experiments (Bobbink, 1991; Willems et al., 1993; Jacquemyn et al., 2003). Several of the experimental studies suggest that the increasing dominance of *Brachypodium pinnatum* is one of the main proximal reasons for the observed species loss (e.g., Bobbink and Willems, 1987). The evidence for a decrease in species richness and the role of N enrichment in this process, however, are not unequivocal. In an N-addition experiment with chalk grassland species, Wilson et al. (1995) did not observe an increasing cover of grasses (such as *Brachypodium*) and a subsequent loss of species diversity. A recent spatial study from Britain also did not give evidence for a negative impact of N deposition on plant species richness in calcareous grasslands (Maskell et al., 2010).

Another limiting nutrient in many ecosystems is phosphorus (P). The input of P into terrestrial ecosystems from weathering and from the atmosphere is usually low, and if N deposition is high, P may become the limiting nutrient and species with efficient P economies may be favoured (Bobbink et al., 2010; Vitousek et al., 2010). Both N and P are likely to play an important role for the species richness and variation in species composition, as evidenced for grasslands by, for example, Kleijn et al. (2008) and Ceulemans et al. (2011, 2013). Compared to N, however, P has received only little attention in the study of vegetation changes in semi-natural terrestrial vegetation.

Apart from a recent analysis of the trends in the frequencies of calcareous grassland species in Germany (Jandt et al., 2011), our study is to our knowledge the first large-scale study of temporal changes in the vegetation of calcareous grasslands. It is a follow-up of a similar analysis conducted in acidic grasslands in North-western Europe (Duprè et al., 2010) where the impact of N deposition on species assemblages and diversity were found to be dramatic. Based on an analysis of historical and recent vegetation data from North-western Germany, we aimed to: (1) examine changes in the species composition and richness in calcareous grasslands over the last 70 years in response to N deposition, (2) compare the temporal trends of species with different life-history traits and ecological strategies, (3) assess the role of P for the species composition and richness in calcareous grasslands, and (4) contrast the results with those obtained in acidic grasslands and discuss the underlying causes for the differences between the two grassland types.

2. Material and methods

2.1. Vegetation data

Plot-scale data from calcareous grasslands were compiled from the sub-oceanic areas of North-western Germany (Fig. 1). More southern and continental regions with a much larger pool of calcareous grassland species were avoided to obtain a vegetation data

Fig. 1. Map of the study areas in North-western Germany from where plots of calcareous grasslands were compiled.