Dise and Stevens 2005 Science in China 48 720-728

Nitrogen Deposition and Reduction of Terrestrial Biodiversity: Evidence from Temperate Grasslands

Nancy B. Dise,[1,2] and Carly J. Stevens,[1,3]

[1] Department of Earth Sciences, The Open University, Milton Keynes, MK7 6AA, UK
[2] Department of Biology, Villanova University, Villanova, PA 19085, USA
[3] Department of Agricultural Science, Imperial College at Wye, Wye, Ashford, TN25 4NJ, UK

ABSTRACT

Biodiversity is thought to be essential for ecosystem stability, function and long-term sustainability. Since nitrogen is the limiting nutrient for plant growth in many terrestrial ecosystems, reactive nitrogen has the potential to reduce the diversity of terrestrial vegetation and associated biota through favouring species adapted to quickly exploiting available nutrients. Although the potential has long been recognised, only recently has enough evidence come together to show beyond reasonable doubt that these changes are already occurring. Linked together, experimental, regional/empirical, and time-series research provide a powerful argument that enhanced deposition of reactive nitrogen across Great Britain, and potentially the rest of Europe, has resulted in a significant and ongoing decline in grassland species richness and diversity.

INTRODUCTION

Native and rare plant species in semi-natural ecosystems are often adapted to low nutrient conditions and can compete successfully only in nitrogen-deficient soils (Grime, 1979). Since nitrogen (N) is the limiting nutrient for plant growth in many terrestrial ecosystems, an excess of reactive N to these ecosystems may reduce plant diversity through favouring species adapted to quick exploitation of available nutrients. Nitrogen may also decrease diversity through factors such nutrient imbalance (e.g., inducing P limitation), soil acidification, or increased susceptibility to diseases or pests (e.g. Phoenix et al. 2003, Power et al., 1998; Brunsting and Heil, 1985). Loss of biodiversity is a central issue in environmental science today – beyond obvious moral, aesthetic and utilitarian arguments (e.g. loss of potential useable products and medicines), a reduction in biodiversity may result in a deterioration of overall ecosystem function such as nutrient retention and sequestration of atmospheric CO_2 (Tilman et al. 1996; Reich et al. 2001).

Due to substantial growth in anthropogenic emission of reactive N through fossil fuel combustion and agriculture over the last ca 50 years, today a major source of N to semi-natural ecosystems is atmospheric deposition. Nearly all of the reactive N from fossil fuel combustion ends up in the atmosphere as NO_x. Fertiliser-produced reactive N (NH_3 and related compounds) may be directly volatilised during application, or may be secondarily released via the volatilised excreta of livestock, especially in intensive units. In both cases reactive N is deposited between tens and hundreds of kilometres from the source. As a result, over the last century the nitrogen content of deposition across many areas of Europe has probably increased by 5 to 10 fold (e.g. Goulding et al. 1998).

Most (>70%) of the excess reactive N in European deposition is NH_4^+ originating from agricultural sources (EMEP, 2000). Thus, the distribution of N deposition across Europe's Atlantic region primarily reflects the intensity of agricultural activity, being highest in the Netherlands, Belgium, Germany and Brittany, reaching local levels as high as 70 kg N ha^{-1} y^{-1} (Dise et al., 1998). Because it is dominated by an extremely diffuse source that is difficult to control, N deposition in Europe has remained constant or has only modestly declined over the last 30 years, unlike sulfur (S) deposition, which has been dramatically reduced due to pollution controls (NEGTAP, 2001). Globally, elevated nitrogen deposition is a significant problem in areas of high-intensity agriculture/livestock or industrialisation, including the eastern USA, many parts of the former Soviet Union and Asia, and more densely populated areas of South America and Africa (Bouwman et al, 2002).

Despite convincing theoretical arguments, it was not until 2004 that enough lines of evidence coincided to provide a powerful argument that terrestrial biodiversity is actually declining due to the production, emission and subsequent deposition of reactive N produced through human activities. This paper briefly outlines this evidence. It is selective and primarily focused on the United Kingdom, and thus is in no way meant to be a comprehensive analysis of nitrogen impacts on terrestrial ecosystems; for this there are several excellent review papers (e.g. Bobbink et al. 1998).

We focus on grasslands for two reasons. Firstly, grasslands are readily measured and manipulated, and they encompass most of the ecological functions and biogeochemical linkages of other terrestrial systems. Equally important is the intrinsic value of grasslands themselves. Grasslands (including shrubland and tundra) cover 40% of the Earth's land surface and are home to almost a billion people (Revenga et al. 1998). In Europe, a disproportionate amount of biodiversity occurs in grasslands (Watkinson and Ormerod, 2001); they are particularly known as valuable habitat for insects and birds, whose diversity has also been documented as declining (e.g. Thomas et al., 2004). In addition, in the UK approximately 60% of lowland grassland, heath and scrub key conservation sites (as identified by Ratcliffe, 1977) receive more than 20 kg N ha^{-1} y^{-1} as atmospheric deposition (Woodin and Farmer, 1993).

In this review we ask two questions:

1. Can atmospheric nitrogen deposition reduce grassland biodiversity?
2. *Is* atmospheric nitrogen deposition reducing grassland biodiversity?

In answering these questions we bring together: 1. experimental N addition studies to sensitive grasslands, 2. a regional study of grassland species richness across the natural gradient of N deposition in Great Britain, and 3. evidence from repeated measurements of the same sites over many years. Taken together, these studies provide a powerful argument that N deposition is significantly damaging the species richness of at least one sensitive terrestrial ecosystem.

1. EXPERIMENTAL N ADDITION STUDIES

Ideally, the way to determine if enhanced levels of reactive nitrogen in deposition are impacting grassland diversity would be to closely monitor experimental plots, in which the only variable is N deposition, over several decades. In reality, the lifespans of both research grants and researchers do not allow this. Thus experimental studies use much larger doses of nitrogen over a shorter time, with the underlying assumption that this effectively mimics much smaller doses of N over a much longer time.

The typical dose of N addition experiments ranges from ca 20 to 200 kg N ha^{-1} y^{-1} (usually as ammonium- or sodium nitrate), or about 5-10 times higher than current ambient N deposition. For an N addition experiment of 100 kg N ha^{-1} y^{-1} over 10 years and assuming that N is not lost in seepage or deep soil layers or volatilised, this is a cumulative 1000 kg N ha^{-1}, or 60 years of deposition of N at 17 kg N ha^{-1} y^{-1}, the average in Europe. Here we consider four such manipulation studies – three in the UK and one in the US – on sensitive acid, neutral and calcareous grasslands.

Park Grass, UK

By far the longest and arguably the most important nutrient manipulation study in the world is the Park Grass nitrogen addition experiment at Rothamsted Experimental Station, Hertfordshire, UK (51° 48'N, 0° 21'W) (Jenkinson *et al.*, 1994). Lawes and Gilbert initiated a range of nitrogen and other nutrient additions in 1856 on an area that had already been under grass for several centuries. Sodium nitrate applied at a rate of 48 kg N ha^{-1} y^{-1} or more led to a rapid disappearance of legumes and many broad-leaved plants. By the first detailed sampling in 1862, 6 years after the beginning of the experiment, marked changes had already occurred, with species numbers decreasing from around 50 to approximately 33 (Jenkinson *et al.*, 1994; Goulding *et al.*, 1998) (Figure 1). After this, species numbers continued to decline in both the N addition sites and the controls in parallel, most likely due to the long-term effect of chronic acid deposition (Goulding *et al.*, 1998). Currently the $NaNO_3$ plots support approximately 20 species, with about 35 in the controls.

A second treatment at Rothamsted was the addition of ammonium sulfate at the same level as the NH_4NO_3 treatments. Over the 150 years of the experiment, this treatment caused a dramatic decline in the soil pH, from 5.8 to 3.5 (Johnson et al., 1986). This 100-fold soil acidification was accompanied by a major reduction in species richness, from ca 50 to only 1 or 2 currently. Thus the $(NH_4)_2SO_4$ treatment served in part to distinguish between the effects of acidification and eutrophication in the N treatments.

Tadham Moor, UK

Tadham Moor (51° 12'N, 2° 49'W) is a pH-neutral, nutrient-poor hay meadow in Somerset, designated as a Site of Special Scientific Interest (SSSI) due to its rich mix of species, including several that are rare or threatened. It has been managed for many decades by mowing for hay followed by stock grazing (Mountford et al., 1993). Because these grasslands are of high value and seen as potentially highly vulnerable to nitrogen deposition, an N-addition experiment was initiated in 1986 to determine whether relatively small doses of nitrogen would impact species richness and composition. N was added as NH_4NO_3 at levels of 25-200 kg N ha^{-1} y^{-1}.

Application of 25 kg N ha^{-1} y^{-1} encouraged the spread of agriculturally productive grasses within 2 years, and 50 kg ha^{-1} y^{-1} significantly reduced species richness within 3 years (Mountford *et al.*, 1993). Fertiliser addition changed the sward to one dominated by grasses, especially *Lolium* and *Holcus*, at the expense of forbs, *Carex* and *Juncus* species (Kirkham and Wilkins, 1994). After 5 years of fertiliser application, the balance of species in the seed bank had been changed in favour of species that were more competitive under fertile conditions (Kirkham and Kent, 1997). At the 100 kg N ha^{-1} y^{-1} level, there was an approximately 30% decline in species richness over 7 years.

The N addition experiments resulted in the recognition that the ecology of these meadows is "sensitive to even small levels of fertiliser application" (Kirkham and Wilkins, 1994). Further study with manipulating other nutrients showed that P limitation also occurs in these grasslands (Kirkham *et al.*, 1996).

Wardlow Hay Cop, UK

Wardlow Hay Cop is a small limestone hill in the Peak District, in Derbyshire (53° 15'N, 1° 44'W). It has a cretaceous calcareous base which is covered in areas with acidic glacial till. This results in a highly variable chemical environment in which soil pH varies from around 6.8 (in areas where only a thin soil covering overlays the limestone) to 4.1 (in till-covered areas, where soils are up to 70 cm deep). The vegetation follows this trend, with typical species-rich calcareous grassland and acidic grassland in close proximity.

A nitrogen addition experiment begun in 1990 took advantage of this heterogeneity with two parallel experiments, one on a calcareous grassland and one on a nearby acid grassland (Morecroft et al. 1994, Carroll et al. 2003). Treatments ranged from 35 to 140 kg N ha^{-1} y^{-1} as NH_4NO_3, an $(NH_4)_2SO_4$ treatment (140 kg N ha^{-1} y^{-1}), and P and glucose treatments (50 and 72 kg ha^{-1} y^{-1}, respectively) to remove P deficiency and microbial carbon limitations, respectively.

After 3 years there was only one significant trend: a decrease in the % cover of the moss *Rhytidiadelphus squarrosus* in the $(NH_4)_2SO_4$ plot on the acid grasslands (Morecroft et al. 1994). After 6 years in the acid grasslands there were significant declines in bryophytes at all N addition levels, and non-significant trends in reduced cover for *Potentilla erecta*, *Festuca ovina*, and *Agrostis spp.* at levels of N addition of 70 kg N ha^{-1} y^{-1} or higher. Trends in increased cover were observed for *Nardus stricta* -- a grass tolerant of highly acidic conditions -- for all treatments, especially the $(NH_4)_2SO_4$ plots.

In the calcareous grasslands, the $(NH_4)_2SO_4$ treatment had the strongest effect, with significant declines in the cover of *Thymus polytrichus* (also at the highest NH_4NO_3 level) and *Carex flacca*, and a significant increase in the cover of *Koelaria macracantha*. Trends toward lower cover with at least one NH_4NO_3 treatment occurred for *Festuca ovina*, *Helicotrichon pratense*, and *Helianthemum nummularium*.

In addition to the population effects, there were clear dose-related increases in shoot N content and N/P ratios and increased rates of N mineralisation and (in the calcareous plots) nitrification rates. Addition of P on the calcareous plots increased cover and growth for forbs and grasses, with a trend toward decreasing cover for sedges. Also in the calcareous plots, the sulfate addition and the two highest NH_4NO_3 treatments were associated with a significant decline in soil pH. This may be due to the addition of the mobile anions sulfate or nitrate (which causes increased leaching of basic cations from the soil), to enhanced rates of nitrification, or to root uptake of NH_4^+ in exchange for H^+. Soil pH did not significantly change in the acid grasslands at any treatment.

Thus, it appears from these ongoing experiments that the highest levels of N addition ($\geq$ 70 kg N ha^{-1} y^{-1}) directly impacted species composition in the acid grasslands, with bryophytes particularly affected. For the calcareous grassland, the primary effect of N addition on species composition was through a significant decline in soil pH. After six years, there appeared to be little direct influence of N on species composition, perhaps due to plant growth in the calcareous grassland being phosphorus limited or co-limited by phosphorus and nitrogen.

Cedar Creek Natural History Area, USA

The Cedar Creek Natural History Area experiments in Minnesota, USA (45° 30'N, 93° 12'W) (Tilman 1987) were begun in 1982 to investigate the importance of prairie grassland diversity on ecosystem properties such as carbon accumulation and nitrogen retention, and the environmental factors that impact diversity. For the latter, atmospheric nitrogen was the major factor investigated. Six different NH_4NO_3 addition treatments ranging from 10 to 272 kg N ha^{-1} y^{-1} were used, and other nutrients were added so that no nutrient deficiencies occurred. The experimental manipulations occurred on three fields abandoned at different time periods: 14, 25 and 48 years before the experiment began in 1982. The oldest 2 fields (B,C) contained primarily C4 native prairie grasses such as *Schizachyrium scoparium*, little bluestem. The youngest field (A) was dominated by C3 species typical of recent disturbance or elevated nutrients, such as the non-native *Agropyron repens*, quackgrass. Thus, the experiment investigated the effect of nitrogen on the species richness of prairie grassland of different successional age.

After 12 years of treatment there was a significant decrease in species richness in all three fields, with an approximately negative exponential treatment-response curve (Wedin and Tilman, 1996) (Figure 2). In all three experiments, *Agropyron repens* increased significantly in absolute and relative abundance with the nitrogen treatments. Significantly decreasing was *Berteroa incana* in Field A, *Rumex acetosella* and *Lespedeza capitata* (a legume) in Field B, and *Schizachyrium scoparium* (native bunchgrass), *Solidago nemoralis, and Sorghastrum nutans* in Field C (Tilman, 1987).
At the 100 kg N ha^{-1} y^{-1} level, there was an approximately 40% decline in species richness over 12 years.

Summary of experimental additions

The results of the experimental N addition studies described above can be summarised as:

- Species richness generally declines by 20-80%.
- The decline in species richness is somewhat dose-dependent (within experiments).
- With N additions of > 70 kg N ha^{-1} y^{-1}, species richness declines within 2-3 years, with lower N additions, a longer time is generally required before significant effects occur (> 10 years).
- Grasses do well.

- Forbs, mosses and sedges do poorly.
- The effect of N is in part dependent on the availability of other potentially limiting nutrients, especially P.
- The decline in soil pH associated with N deposition may make a significant contribution to the reduction in species richness and changes in species composition.
- The relative importance of soil acidity versus eutrophication depends on factors such as the soil buffer capacity and the availability of other nutrients.

2. REGIONAL GRADIENT STUDY

Despite clear evidence from N-addition experiments that increased deposition of atmospheric N would reduce terrestrial plant biodiversity, such changes have been difficult to detect on the ground. This is primarily due to the large number of interacting factors that control plant community composition. Thus, until recently, there was no evidence that widespread biodiversity reduction due to regional air pollution was actually occurring. Two methods have been used to investigate this question: regional gradients of N deposition as a proxy for a time series, and revisiting marked plots over time. In both, differences in species richness or composition are evaluated to determine if these are consistent with the expected effects of chronic nitrogen deposition.

Stevens et al. (2004) surveyed a grassland community in Great Britain to determine if any significant variability in plant species richness could be detected and, if so, related to regional-scale levels of atmospheric pollution (inorganic N, inorganic S) deposition. Great Britain is an ideal location for such a study. It has well-described plant communities, a relatively homogeneous climate and land use, and a steep pollution gradient covering the full range of N deposition in North America and more than half the range in Europe.

Stevens et al. 2004 chose an *Agrostis-Festuca* acid grassland, a type common throughout Europe, Australia and North America that makes up economically valuable pastureland. Sixty-eight sites were sampled in 2×2 m quadrats (5 replicate quadrats per site) along the gradient of atmospheric N deposition (5-35 kg N ha^{-1} y^{-1} wet + dry deposition) during the summers of 2002 and 2003. For each site they compiled a dataset of the potential drivers on terrestrial species richness (Table 1). These included nine chemical environmental factors, nine physical environmental factors and two human modifications. These variables were entered into a stepwise multiple regression with site species richness as the dependent variable.

Table 1. Variables examined for relationships to plant species richness (number of species per quadrat) in Stevens et al. 2004.

Variable	Abbreviation	Range
Total inorganic nitrogen deposition (kg N ha^{-1} y^{-1})	Ndep	6.2 – 36.3
Total deposition $NH_3 + NH_4^+$ (kg N ha^{-1} y^{-1})	N-red	2.8 – 31.2
Total deposition $NO + NO_2 + NO_3^-$ (kg N ha^{-1} y^{-1})	N-ox	2.2 – 12.6
Sulphate deposition (kg SO_4^{2-}- S ha^{-1} y^{-1})	Sdep	6.6 – 28.7

Acid deposition (total N + total S, kg ha^{-1} y^{-1})	Aciddep	13.0 – 61.4
Topsoil pH (A horizon)	Top pH	3.7 – 5.5
Subsoil pH (30-40 cm)	Sub pH	3.3 – 5.7
Mean annual temperature (°C)	Temp	6.6 – 10.6
Mean annual precipitation (mm)	MAP	594 - 3038
Mean annual actual evapotranspiration (mm)	AE	35.7 – 49.3
Mean annual potential evapotranspiration (mm)	PE	35.8 – 54.3
Mean annual soil moisture deficit (mm)	SMD	3.4 – 51.4
Altitude (m)	Alt	15- 692
Litter cover (%)	Lit	0 - 24
C:N (by mass)	CN	13.3 – 30.2
%N (by mass)	%N	0.1 – 1.6
Slope (°)	Slope	0 - 60
Aspect (°)	Asp	**0 - 359**
Grazing (1 = high intensity – 3 = low intensity)	Graz	**1 - 3**
Enclosures (1 presence, 0 absence)	Encl	**0 - 1**

Stevens et al. found a strong, highly significant negative linear relationship between N deposition and species richness (Fig 3). Of the variables in Table 1, total deposition of inorganic N was the most important predictor of species richness, explaining over half of the variation in the data (Fig. 3):

Plant Species Richness = 23.3 – 0.408(*Ndep*) ($r^2 = 0.55$, N=68, $p<0.0001$) (Eq. 1)

Equation 1 indicates that for every 2.5 kg ha^{-1} y^{-1} of inorganic N deposited on an acid grassland, a mean of 1 additional species is excluded from a randomly placed 4 m^2 quadrat.

Topsoil pH, which ranged from 3.7 to 5.5, was the next most important regional-scale variable: at any level of N deposition, sites with a higher soil pH showed on average higher species richness:

Plant Species Richness = 6.63 – 0.316(*Ndep*) + 3.40(*Top pH*) (r^2=0.61, N=68, $p<0.004$) (Eq. 2)

Soil pH is in part due to the local site characteristics (parent material, organic matter content, management history) and in part to the long-term rate of acid deposition.

Canonical correspondence analysis showed a consistent loss of certain species: the forbs *Plantago lanceolata* (ribwort plantain), *Campanula rotundifolia* (harebell), and *Euphrasia officinalis* (eyebright); the shrub *Calluna vulgaris* (heather), and the moss *Hylocomium splendens* (mountain fern moss). All of these species have been shown to decline under experimental N applications or are considered indicators of infertile sites. Surprisingly, the grass *Molinia caerulea* (purple moor grass) also tended to be reduced in lower-diversity plots, although it is commonly considered to benefit from enhanced N deposition (e.g. Bobbink et al. 1998). Aerts et al. (1990) showed in N addition experiments that *Molinia* declined at intermediate N additions (100 kg N ha^{-1} y^{-1}) but became dominant at higher N additions. It is possible that the UK regional data reflect this intermediate situation. These 6 species comprise 21% of the maximum species number.

The ‘critical load’ for N deposition for acid grasslands (exposure to a pollutant below which significant harmful effects do not occur according to present knowledge; Nilsson and Grennfelt, 1988) is 10-20 kg N ha^{-1} y^{-1} (Achermann and Bobbink, 2003), similar to the mean N deposition rate of the UK and central Europe (17 kg N ha^{-1} y^{-1}). Figure 3 predicts that at this level of chronic N deposition, species richness in UK acid grasslands has already been reduced by about 25% (taking a species richness of 21.3 at 5 kg N ha^{-1} y^{-1} to be the ‘pristine’ condition).

When linked together, experimental N addition experiments and regional surveys can yield estimates of the number of years required to reach the pattern shown in Figure 3. We start with a predicted species richness reduction of 25% at the European average N deposition. Then, using an average of a 3.5% reduction in species richness for each 100 kg N ha^{-1} added over the course of the N addition experiments of Wedin and Tilman (1996) and Mountford et al. (1993), the total amount of N required to decrease species richness by 25% is 714 kg N ha^{-1}. At 17 kg N ha^{-1} y^{-1}, the time to reach 714 kg N ha^{-1} is 42 years. Although this exercise entails numerous assumptions (e.g. N deposition has a fully cumulative effect on vegetation and has been constant over time), most of which make it a low estimate, a time frame of 40-50 years is consistent with the enhanced emission of reactive N beginning around the start of the 20th century, and accelerating in its latter half.

3. CHANGES IN GRASSLAND SPECIES RICHNESS OVER TIME

The N addition experiments showed that the impact of N deposition on a grassland is influenced by numerous factors, especially the type of community, the amount and duration of the N input, the management regime, and soil qualities such as buffering capacity and nutrient status. Climate also exerts a major influence on species response to nitrogen, in part by determining the relative importance of nitrogen as a limiting factor for growth.

With nitrogen deposition elevated for more than 50 years in some areas, it should be possible to detect species changes in some of the most vulnerable grassland ecosystems. This is very rare, however. A major problem is the need for precise long-term monitoring of sites, and the requirement that other factors such as land use do not change significantly. There are nonetheless a few cases where either the nitrogen input on a sensitive ecosystem has been so high for so long, or the monitoring has been so precise, that we can state beyond reasonable doubt that species changes have occurred consistent with atmospheric N-driven eutrophication or acidification.

In the Netherlands, expansion of grasses such as *Brachypodium pinnatum* and *Molinia caerulea* at the expense of more nitrogen-sensitive plants such as heather and forbs is well documented (e.g. Heil and Diemont, 1983, Bobbink et al. 1998). Plants such as *Brachypodium* and *Molinia* combine efficient uptake of limiting nutrients such as N and P with the ability to grow rapidly and therefore competitively exclude other species

In 2004, a landmark study was published showing a major loss of diversity of plants, birds and butterflies in Great Britain (Thomas et al. 2004). The study used six large national-scale censuses covering a period of 20 to 40 years, and found that over that time period 28% of native plants, 54% of native birds and 78% of native butterflies had declined. Land use change (a large increase in high-intensity agricultural and urban/suburban development) likely accounted for much of the decline in species, but regional air pollution was also thought to play a role.

A second UK study provided strong evidence for N deposition as a driving force for vegetation change (DEFRA, 2003). National surveys of permanent plots in 1978, 1990 and 1998 showed increases in Ellenberg indicator scores for fertility (Ellenberg *et al.*, 1991 re-calculated for use in Great Britain by Hill *et al.*, 2000) in almost all vegetation types across the British landscape, with infertile grasslands and moorland grass mosaics showing the largest increases. The resurveys also showed a 23% reduction in the species richness of infertile grasslands. This trend is of even greater concern when considering that, if the rate of change observed between 1990 and 1998 remained constant, it would take only 53 years for the average fertility score of infertile grasslands to reach that of fertile grasslands (Smart *et al.*, 2003).

CONCLUSION

The combination of nitrogen addition experiments, a national gradient study, and re-surveys of plots over time agree that not only is there the *potential* for a decline in species richness as a result of nitrogen (N) deposition, but also that these changes are actually occurring in the UK. Species most deleteriously impacted by N deposition in the experimental studies are low-growing forbs, mosses and sedges, which are generally adapted to low nutrient levels and are unable to compete with grasses for light or space. A series of surveys separated by intervals of ca 10 years show that these vegetation types, and the insects and birds that depend on them, are disproportionally declining in the UK. In addition, they are the same types identified as missing or reduced in the gradient study. Both the experimental and the gradient studies show that species richness declines due both to the direct effects of nitrogen and to soil acidification. The relative importance of each factor will likely vary with ecosystem properties such as the soil buffering capacity and the availability of other nutrients.

Combining the experimental and the gradient studies gives a time scale of at least 40 years to reach the observed level of biodiversity reduction. Although some species are likely to return after a relatively short period if nitrogen deposition were significantly reduced, the return to a condition of high species richness may not be achieved in the foreseeable future, and only with major cuts in the emission of reactive nitrogen. These declines in species richness form part of an increasingly worrying trend of local extinctions in the UK as a result of changes in the landscape and the atmosphere brought about by humans. Finally, the declines in diversity are unlikely to be restricted to grasslands, but are potentially occurring throughout numerous semi-natural habitats in Europe and the world.

ACKNOWLEDGEMENTS

The gradient study (Stevens et al. 2004) was funded the Open University Research Development fund as a Ph.D. studentship to CS. We would like to thank the research group of Prof. David Fowler (Natural Environment Research Council (NERC) Centre for Ecology and Hydrology, Edinburgh) for providing nitrogen deposition data, and NERC for an annual honorarium to CS.

Figure 1. Changes through time in the number of species on the Park Grass Experiment. ▼ control; ■ sodium nitrate; ▲ ammonium sulphate, no lime; ♦ ammonium sulphate with lime (from Goulding *et al.*, 1998 reproduced with the permission of the New Phytologist Trust).

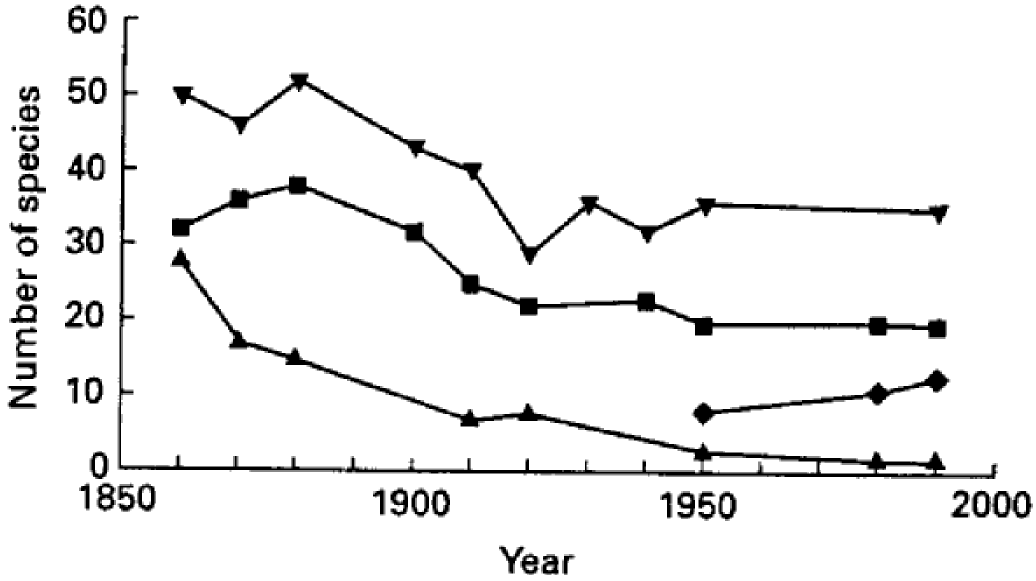


Figure 2. Number of vascular plant species found in 0.3-m^2 vegetation samples in Minnesota grasslands after 12 years of N addition (reprinted with permission from Wedin and Tilman, SCIENCE 274: 1720-23 Copyright 1996 AAAS).

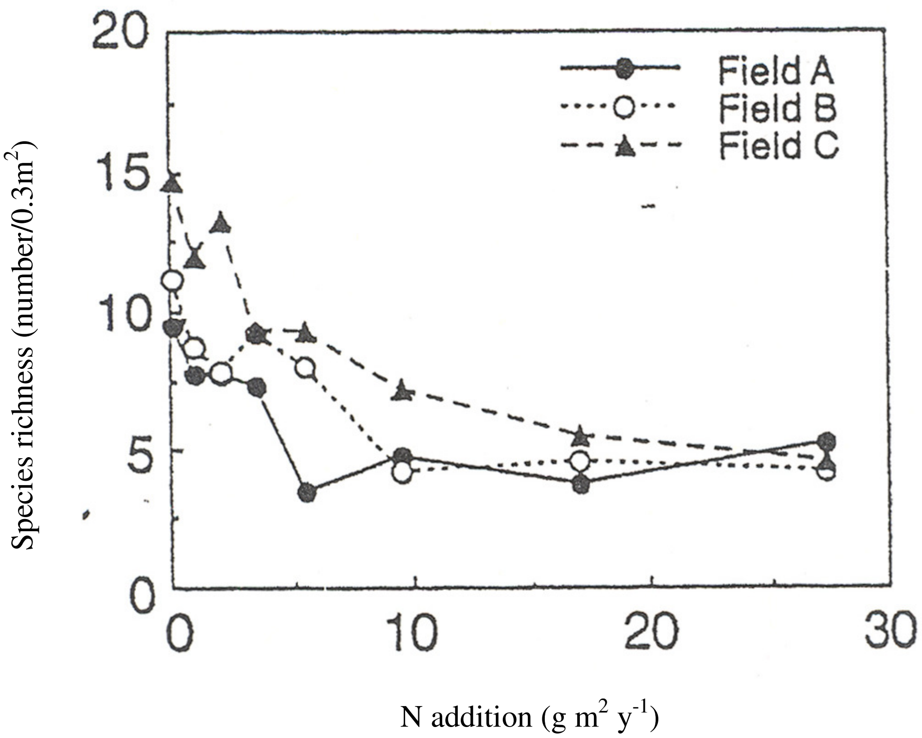
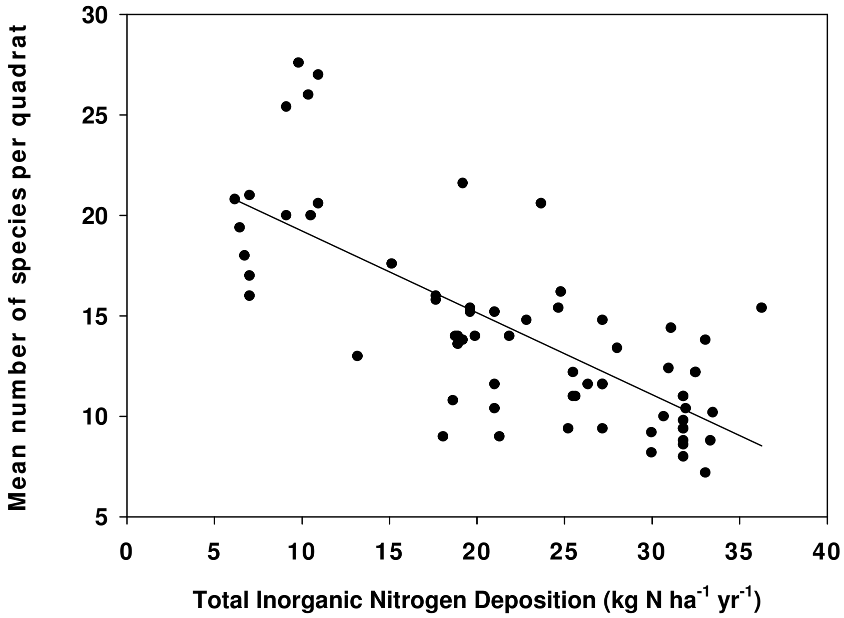


Figure 3. Decline in the species richness of acid grasslands along a gradient of N deposition (from Stevens et al, 2004).



References

Achermann B. and Bobbink, R. (eds) **2003**. *Empirical critical loads for nitrogen*. Environmental documentation no 164. Swiss Agency for the Environment, Forests and Landscape, Berne.

Aerts, R., Berendse, F., de Caluwe, H., Schmitz, M. **1990**. Competition in heathland along an experimental gradient of nutrient availability. *Oikos* **57**: 310-318.

Bobbink, R., Hornung, M., and Roelofs, J. G. M., **1998**. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology* **86**:717-738.

Bouwman, A. F., van Vuuren, D. P., Derwent, R. G., and Posch, M., **2002**. A global analysis of acidification and eutrophication of terrestrial ecosystems. *Water, Air and Soil Pollution* **141**:349-382.

Brunsting, A. M. H., and Heil, G. W., **1985**. The role of nutrients in the interactions between a herbivorous beetle and some competing plant species in heathlands. *Oikos* **44**:23-26.

Carroll, J.A., Capporn, S.J.M., Johnson, D., Morecroft, M.D., Lee, J.A. **2003**. The interactions between plant growth, vegetation structure and soil processes in semi-natural acidic and calcareous grasslands receiving long-term inputs of simulated pollutant nitrogen deposition. *Environmental Pollution* **121**: 363-376.

DEFRA (Department of Envirnment, food and rural affairs), **2003**. *A biodiversity strategy for England. Measuring progress: Baseline assessment*. Department for Environment, Food and Rural Affairs, London.

Dise, N.B., Matzner, E. and Gundersen, P. **1998**. Synthesis of nitrogen pools and fluxes from European forest ecosystems. *Water, Air and Soil Pollution*, **105**: 143-154.

Ellenberg, H., Weber, H. E., Dull, R., Wirth, V., Werner, W., and Paulissen, D., **1991**. Zeigerwerte von pflanzen in mitteleuropa *Scripta Geobotanica* **18**:1-248.

EMEP (Co-operative Programme for Monitoring and Evaluation of the Long-Range Transmission of Air pollutants in Europe), **2000**. *Transboudary acidification and eutrophication in Europe*. Research Report no. 101, Norwegian Meterological Institute.

Goulding, K. W. T., Bailey, N. J., Bradbury, N. J., Hargreaves, P., Howe, M., Murphy, D. V., R., P. P., and Willison, T. W., **1998**. Nitrogen deposition and its contribution to nitrogen cycling and associated soil processes. *New Phytologist* **139**:49-58.

Grime, J. P., **1979**. *Plant strategies and vegetation processes*, Wiley; London.

Heil, G. W., and Diemont, W. H., **1983**. Raised nutrient levels change heathland into grassland. *Vegetatio* **53**:113-120.

Hill, M. O., Roy, D. B., Mountford, J. O., and Bruce, R. G. H., **2000**. Extending Ellenberg's indicator values to a new area: An algorithmic approach. *Journal of Applied Ecology* **37**:3-15.

Jenkinson, D. S., Potts, J. M., Perry, J. N., Barnett, V., Coleman, K., and Johnston, A. E., **1994**. Trends in herbage yields over the last century on the Rothamsted long-term continuous hay experiment. *Journal of Agricultural Science* **122**:365-374.

Johnson, A.E., Goulding, K.W.T. and Poulton, P.R. **1986**. Soil acidification during more than 100 years under permanent grassland and woodland at Rothamsted. *Soil use and management* **2**: 3-10.

Kirkham, F. W., and Kent, M., **1997**. Soil seed bank composition in relation to the above-ground vegetation in fertilized and unfertilized hay meadows on a Somerset peat moor. *Journal of Applied Ecology* **34**:889-902.

Kirkham, F. W., Mountford, J. O., and Wilkins, R. J., **1996**. The effects of nitrogen, potassium and phosphorus addition on the vegetation of a Somerset peat moor under cutting management. *Journal of Applied Ecology* **33**:1013-1029.

Kirkham, F. W., and Wilkins, R. J., **1994**. The productivity and response to inorganic fertilizers of species rich wetland hay meadows on the Somerset moors: Nitrogen response under hay cutting and aftermath grazing. *Grass and Forage Science* **49**:152-162.

Morecroft, M. D., Sellers, E. K., and Lee, J. A., **1994**. An experimental investigation into the effects of atmospheric deposition on two semi-natural grasslands. *Journal of Ecology* **82**:475-483.

Mountford, J. O., Lakhani, K. H., and Kirkham, F. W., **1993**. Experimental assessment of the effects of nitrogen addition under hay-cutting and aftermath grazing on the vegetation of meadows on a Somerset peat moor. *Journal of Applied Ecology* **30**:321-332.

NEGTAP (National expert group on transboundary air pollution) **2001**. *Transboundary air pollution: Acidification, eutrophication and ground-level ozone in the UK*. Edinburgh, CEH.

Nilsson, J. and Grennfelt, P., (eds) **1988**. *Critical Loads for Sulphur and Nitrogen*; NORD 1988:15, Nordic Council of Ministers: Copenhagen, Denmark.

Phoenix, G. K., Booth, R. E., Leake, J. R., Read, D. J., Grime, P., and Lee, J. A., **2003**. Effects of enhanced nitrogen deposition and phosphorus limitation on nitrogen budgets of semi-natural grasslands. *Global Change Biology* **9**:13.19-1231.

Power, S.A. Ashmore, M.R. and Cousins, D.A. **1998**. Impacts and fate of experimentally enhanced nitrogen deposited on a British Lowland Heath. *Environmental Pollution*, **102**, 27-34.

Ratcliffe, D. A., **1977**. *A nature conservation review*, Cambridge University Press; Cambridge.

Reich, P.B., Knops, J., Tilman, D., Craine, J., Ellsworth, D., Tjoelker, M.., Lee, T., Wedin, D. et al. **2001**. Plant diversity enhances ecosystem responses to elevated CO2 and nitrogen deposition. *Nature* **410**: 809-812.

Revenga, C., Murray, S. and Abramovitz, J. and Hammond, A**. 1998**. *Watersheds of the World: Ecology and Vulnerability*. Washington DC: World Resources Institute

Smart, S. M., Robertson, J. C., Shiels, E. J., and Van de Poll, H. M., **2003**. Locating eutrophication effects across British vegetation between 1990 and 1998 *Global Change Biology* **9**:1763-1774.

Stevens, C. J., Dise, N. B., Mountford, J. O., and Gowing, D. J. **2004**. Impact of nitrogen deposition on the species richness of grasslands, *Science* **303**:1876-1879.

Thomas, J. A., Telfer, M. G., Roy, D. B., Preston C. D., Greenwood, J. J. D., Asher, J., Fox, R., Clarke, R. T. and Lawton, J. H. **2004.** Comparative losses of British butterflies, birds and plants and the global extinction crisis, *Science* **303** 1879-1881.

Tilman, D. **1987**. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monogrographs* **57**: 189- 214.

Tilman, D., Wedin, D., and Knops, J. **1996**. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**: 718-720.

Watkinson, A.R. and Ormerod, S. J. **2001**. Grasslands, grazing and biodiversity: editors' introduction. *Journal of Applied Ecology* **38**: 233-237.

Wedin, D.A. and Tilman, D. **1996**. Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* **274**: 1720-23.

Woodin, S. J. and Farmer, A. M. **1993**. Impacts of sulphur and nitrogen deposition on sites and species of nature conservation importance in Great Britain. *Biological Conservation* **63**: 23-30.