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Whole Ecosystem Nitrogen Manipulation: An Updated Review

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Foreword

This document reviews research undertaken in the UK and across Europe involving nitrogen manipulation experiments in natural and semi-natural ecosystems, updating an original review report from 1997. The experiments are essential to demonstrate and to improve our understanding of the ecological effects of nitrogen deposition, arising from the air pollutants nitrogen oxides and ammonia. Since the initial review two major pieces of work, the Countryside Survey 2000, and the New Plant Atlas of British and Irish Flora (2002), have revealed growing evidence that nitrogen deposition is contributing to a range of ecological changes in semi-natural habitats across the UK. Also since the review, the National Expert Group on Transboundary Air Pollution (NEGTAP 2001) has provided a comprehensive update regarding emissions, deposition and impacts of nitrogen oxides and ammonia, including an assessment of prospects in 2010.

Between 1990 and 2000, emissions of ammonia fell by about 5% and nitrogen oxides by 40%. Deposition decreased by 16%, reflecting the dominance of UK deposited nitrogen derived from ammonia. Further emissions reductions are planned for 2010, under the UN/ECE Gothenburg Protocol and the EC National Emission Ceilings Directive. However, despite progress in cutting emissions, nitrogen deposition will continue to be a threat to significant areas of ecosystems. It is estimated that by 2010 critical loads for eutrophication will be exceeded in 20% of UK 1 km² grid squares with sensitive grassland and 40% with heathland (NEGTAP 2001).

Clearly, the issue of nitrogen deposition continues to raise serious concerns for the foreseeable future. In light of this, it was considered an opportune time to update the nitrogen manipulation review of 1997. The report provides a comprehensive updated synthesis of the experimental work in this area. It should prove invaluable for those in the research field, for conservation managers and for those responsible for developing and implementing nitrogen reduction policies.

The original study was funded by English Nature in 1997 with the update sponsored by Department for Environment, Food and Rural Affairs and published by the Joint Nature Conservation Committee as a collaborative undertaking.

Simon Bareham, Countryside Council for Wales (CCW)
and
Alison Vipond, Department for Environment, Food and Rural Affairs (Defra)
Executive Summary

1. Over the past two decades, concern over the effects of atmospheric nitrogen deposition on terrestrial ecosystems has led to the instigation of a number of field manipulation studies. These were reviewed in an earlier report, commissioned by English Nature. This review updates and revises that earlier report, based on a comprehensive review of all relevant published literature since 1997.

2. The design of experimental manipulation studies has been carefully evaluated, and only studies which meet specific criteria have been considered in this review.

3. This revision includes an interpretation of new data from a number of important long term field experiments in the UK, as well as additional information on interactions between nitrogen deposition and habitat management. Furthermore, in light of recent assessments that UK nitrogen emissions have stabilised and, in the case of nitrogen oxides, even begun to decline, this updated review also considers studies which have looked at rates and indicators of ecosystem recovery.

4. Nitrogen manipulation experiments in forest ecosystems have shown a relationship between deposition inputs and a range of effects. However, the effects of different manipulation studies are highly variable, depending on factors such as soil type, deposition history, stand age, and various biotic interactions.

5. Reported responses include both increases and decreases in tree growth, improvements or imbalances in foliar nutrition, increased incidence of pests and pathogens, and changes in the root system. Soil biology and chemistry are also affected in forested ecosystems, with functional changes in nutrient cycling widely reported; acidification and eutrophication lead in several studies to increased leaching of base cations and increased availability of aluminium and hydrogen cations.

6. Changes in the species composition of the ground flora, mycorrhizae and macro-fungi have been found in several studies, with a general increase in more nitrophilous species.

7. Despite differences in both soil type and climate, responses of Calluna-dominated heathland and moorland ecosystems to N addition in the UK have been fairly consistent. Early responses include increased Calluna shoot growth, canopy height, canopy density, flowering and litter production, whereas prolonged exposure results in reduced root:shoot ratios and an acceleration of the Calluna life cycle.

8. In both UK and continental European experiments, increased nitrogen deposition has been related to increased vulnerability to biotic and abiotic stresses, such as frost, drought and herbivory. Effects on mycorrhizae are varied, with both increases, decreases and no change reported in response to nitrogen. Observed increases in soil microbial activity and biomass, and consequent effects on decomposition and mineralisation rates, have implications for the turnover and
availability of both nitrogen and phosphorus. Differences between immobilisation and mineralisation rates following N addition appear to reflect the degree of nitrogen saturation of a heathland.

9. In grassland ecosystems, nitrogen additions over 5-10 years have resulted in changes in community composition. Lichens, bryophytes forbs and dwarf shrubs are frequently decreased, while grasses typically increase in dominance. These changes are generally associated with a reduction in species richness and diversity of grassland communities following nitrogen addition.

10. Evidence that nutrient cycling may be affected by increased nitrogen availability has also been found for grasslands: Nitrogen mineralisation rates and soil bacterial biomass and activity have increased in response to nitrogen addition. Whilst many similarities in response exist between acidic and calcareous grasslands, the former are typically more vulnerable to the acidifying effects of nitrogen (particularly reduced N) inputs, while interactions with phosphorus availability are important in the latter.

11. In bog ecosystems, nitrogen addition improves growth and survivorship of some moss species, and decreases that of others, with consequent shifts in bryophyte species dominance. In the longer term, it may also cause a reduction in diversity as bryophytes and other low-growing plants are out-shaded by taller species, including grasses. These changes may be related to penetration of nitrogen through the moss layer into the rooting zone, as the capacity to immobilise inputs is exceeded.

12. The few data available on fen ecosystems indicate that high levels of nitrogen deposition cause changes in community composition, with a reduction in species diversity and bryophyte biomass. Changes in species composition and tissue chemistry are also reported for tundra ecosystems.

13. Overall, there are some similarities in response between different ecosystem types, as well as some common mechanisms underlying the observed changes. Nitrogen deposition typically alters the competitive ability of many plant species, resulting in a shift towards more N-tolerant species. The response of a number of species groups is similar across a range of ecosystems, with a general pattern emerging for a reduction in forbs and dwarf shrubs and an increase in grasses.

14. Bryophytes and lichens appear to be particularly sensitive components of most ecosystems.

15. Although not all experiments have reported shifts in community composition in response to nitrogen addition, results consistently suggest a disruption of normal plant and microbial physiology and/or function. Changes in, for example, foliar chemistry or microbial activity may thus be early indicators of the potential for deleterious responses at the community or ecosystem level, in the longer term.

16. The importance of other limiting nutrients, particularly phosphorus, and interactions with habitat management, are major issues for both grasslands and heathlands.
17. Although there are relatively few experiments which have aimed to assess the rate of recovery from ecosystem eutrophication, there is convincing evidence that many ecosystem effects may persist for many years, with recovery only occurring over time scales of many decades, if at all. Indeed, the loss of species from more sensitive ecosystems (such as bogs or tundra systems) may prevent their re-establishment over any realistic time scale, in the absence of active re-introduction and restoration measures.

18. The evidence from nitrogen manipulation experiments demonstrates a significant cause for concern over the impacts of nitrogenous pollutants on sites of nature conservation value. Given the very slow natural rates of recovery once changes in species composition have occurred, and the costs of management interventions to accelerate this process, there is a clear need for a precautionary approach to minimise the risk to sensitive communities across the UK.

19. This review has identified a number of gaps in current knowledge and highlights the need for further research to improve understanding of the responses of the diverse range of (semi-)natural ecosystems in the UK to nitrogen, and to provide a more informed basis for assessment of appropriate critical loads to prevent long-term effects.
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2.2. Lowland Heathland Ecosystems

A lowland heath habitat has been defined as an open landscape generally occurring on nutrient poor, acidic sandy soils below 300 metres in altitude (Gimmingham 1972) and is characterised by the presence of dwarf shrubs of the heather family, notably Calluna vulgaris, Erica cinerea and Erica tetralix. Heathland habitat in European terms is restricted by climate, as lowland heath requires the ‘oceanic climate’ of the western seaboard of the continent (Aerts 1993). Consequently, lowland heath habitats are found in the British Isles, southern Scandinavia, Denmark, north-west Germany, The Netherlands, Belgium, western France and the north and west of the Iberian Peninsula.

There is clear evidence of a loss of Calluna vulgaris and Erica tetralix dominated dry and wet lowland heath in both the UK and other European countries over the last few decades (Pitcairn et al. 1995, Bunce 1989). In the UK lowland dry heath is becoming increasingly rare and is of considerable conservation importance. The transition of many areas of heathland to grassland cannot be explained solely by moves away from the traditional management regimes of burning, grazing and sod cutting (Bobbink and Roelofs 1995, Pitcairn et al. 1995). It is believed that increases in nitrogen deposition, combined with stress and disturbance factors, are the trigger for the change of lowland heath ecosystems into grasslands, as a result of the opening up of the Calluna canopy. Nitrogen manipulation experiments can provide evidence of whether current levels of atmospheric nitrogen deposition can be held responsible for the observed transition of heather-dominated to grass-dominated vegetation. A large number of heathland nutrient manipulation experiments have been undertaken, especially in The Netherlands and Denmark, but with few in the UK. Those studies in which nitrogen was the only nutrient manipulated have their experimental details listed in Table 2.3. Detailed descriptions of the results of those experiments which applied nitrogen at a rate representative of current atmospheric deposition levels (<50 kg N ha⁻¹ yr⁻¹) are given in Table 2.4.

UK studies

In the UK, lowland heath nitrogen manipulation experiments have been undertaken at two locations, Thursley Common in Surrey and Budworth Common in Cheshire. Thursley Common has been an active nitrogen manipulation experimental site since 1989 and receives an estimated background deposition of 10-15 kg N ha⁻¹ yr⁻¹ (Power, unpublished data). To date, three investigations have been undertaken at Thursley, the latter two of which are ongoing:

- Nitrogen addition from 1989 – 1996 at a rate of 0, 7.7, 15.4, or 0/15.4 kg ha⁻¹ yr⁻¹ (in alternate years).
- Nitrogen addition ( 0 or 30 kg N ha⁻¹ yr⁻¹) following management, since 1998.
- A recovery experiment following cessation of nitrogen additions in 1996.

The Budworth Common lowland heath site was established in 1996. The experimental site was dominated by building phase C. vulgaris. Nitrogen additions, in the form of ammonium nitrate, have been applied at two week intervals at 0, 20, 60 and 120 kg N ha⁻¹ yr⁻¹. The main aim of the investigation was to examine the impacts of elevated nitrogen deposition and drought stress on young, actively growing plants.
No changes in species composition were observed in the *C. vulgaris*-dominated experimental site at Thursley Common following seven years of nitrogen additions (Power *et al.* 1998a, 1995), nor even after opening of the dwarf shrub canopy following management after nitrogen additions ceased. However, changes in the growth, flowering and phenology of *C. vulgaris* were numerous. The canopy height and density were both increased with nitrogen addition, canopy height in the highest nitrogen addition treatment being as much as 50% taller than control plots after six years. At the highest nitrogen addition (15.4 kg N ha⁻¹ yr⁻¹) increases in shoot length were as much as 90% greater than control plot shoots. The increased shoot growth was not reflected in root growth, and a reduction in the root:shoot ratio was inferred. Increases in canopy height and density were also seen in studies carried out in The Netherlands, where the canopy was not opened (Bobbink *et al.* 1996). A destructive harvest carried out at the end of the seven year experiment revealed significant treatment effects on the biomass and chemistry of both above-ground vegetation and litter (Power *et al.* 1998a). Furthermore, a nitrogen budget for the site showed that most of the experimentally added nitrogen had accumulated in the litter and humus layers of the soil, suggesting the potential for long term, persistent effects of the accumulated nitrogen.

An additional study carried out at Thursley Common examined whether nitrogen addition could result in increased sensitivity of *C. vulgaris* to abiotic and biotic stress (Power *et al.* 1999b). In plots which received 15.4 kg N ha⁻¹ yr⁻¹, there was a trend towards higher foliar nitrogen concentration; in some years this trend was statistically significant. *C. vulgaris* shoots from the highest nitrogen addition plots showed signs of decreased resistance to frost injury in April, although not in November. However, this was at temperatures much below those normally experienced at the field site.

Enhanced foliar nitrogen concentrations have also been noted during the current investigation at Thursley Common. Significant differences between nitrogen addition and control plots were observed in October 1998 and August 1999. Investigations of soil chemistry at Thursley Common by Barker (2001) and Power *et al.* (1995, 1998a) found that soil pH was significantly reduced from 4.0 to 3.8 in the top 5 cm of ammonium sulphate treated plots in comparison to the control plots. Despite these changes, the concentration of ammonium and nitrate leached from nitrogen addition plots did not differ from that of control plots, and there was no difference in cation (Ca, Mg, K and Na) leaching. Litter production and degradation were also significantly increased following post management nitrogen additions. Such increases may have a long term effect on nutrient cycling and accumulation in these ecosystems (Berendse 1990).

The ongoing nitrogen addition study at Thursley Common enables the effect of different management regimes on heathland response to enhanced atmospheric deposition to be determined. The managements consisted of a low intensity mow, a management burn, a high intensity mow and a simulated accidental burn, representing a gradient of increasing intensity (and N removal) from the system. Full details of the managements are provided in Barker (2001). The results of previous investigations at this site have shown that experimental nitrogen additions have been mainly retained in the soil (Power *et al.* 1998a). The use of different management techniques was therefore designed to produce a gradient of nitrogen removal from the heath. As seen in several other nitrogen manipulation experiments, shoot growth, flowering, litter production and foliar nitrogen concentrations were increased in response to nitrogen addition. There was some evidence of an interaction between nitrogen and management treatments; the intensively managed plots (high mow and simulated accidental burn) responded proportionally more to atmospheric inputs of nitrogen (Power *et al.* 2001). A tentative conclusion was that, during the investigation, higher intensity managements which removed a larger
proportion of stored nitrogen from the heathland may be more effective at reducing absolute plant growth responses to nitrogen. However, further investigation is being undertaken to ascertain the persistence of this effect.

Any form of management opens up the *C. vulgaris* canopy which may enable grass species to become established; however a conflict exists between adequate nutrient removal and the formation of gaps which facilitate grass invasion. As would be expected, the management which resulted in the greatest damage to *C. vulgaris* root stocks, i.e. the simulated accidental burn, resulted in the highest invasion of grass species. These plots also had the greatest increase in seedling invasion in response to nitrogen addition (Power *et al.* 2001), showing a further significant interaction between nitrogen and management treatments. During the investigation both nitrogen addition and habitat management significantly affected rates of decomposition. Rates were elevated in the low intensity mow and management burn, in comparison to the more intensive managements, and the fastest rate was observed in the low intensity mow which received additional nitrogen (Barker 2001, Power *et al.* 2001). Since the quality of the litter used was uniform, the effects seen must have been mediated via the soil environment (Power *et al.* 2001). Therefore, the more intensive managements which removed litter/humus seemed to be more effective at maintaining a lower nutrient environment during the three years of subsequent nitrogen additions.

The present study at Thursley Common also incorporates a recovery experiment, to monitor ecosystem recovery following the cessation of nitrogen addition. The investigation showed that historically high levels of atmospheric nitrogen deposition can continue to have a significant impact on lowland heath for some time following a reduction in deposition (Barker 2001). For example, the former high nitrogen plots had significantly increased shoot growth and total soil nitrogen content, as well as a lower pH than the control plots three years after cessation of nitrogen additions. There was also evidence to suggest that management can have a substantial impact on heathland recovery following a reduction in deposition inputs. The management treatments which removed a greater proportion of the organic nitrogen stores from the system were shown to reduce the magnitude of the carry over effect of former nitrogen applications. For example, shoot growth and height of the *C. vulgaris* canopy in plots which previously received additional nitrogen were lower following the simulated accidental burn than following the low intensity mowing management.

The nitrogen manipulation experiment at Budworth Common in Cheshire began in 1996. Nitrogen was applied as ammonium nitrate at rates of 0, 20, 60 and 120 kg N ha\(^{-1}\) yr\(^{-1}\). A drought was imposed on half of the plots from spring to autumn 1997. Shoot nitrogen content was found to vary with season, however, there were highly significant differences between the nitrogen contents of shoots in the early stages of the experiment, prior to the start of the drought treatment. After ten months of N additions the shoot nitrogen concentrations were directly proportional to application rates, varying between 15 to 20 mg g\(^{-1}\) in the lowest and highest nitrogen treatments respectively (Cawley 2001). However, there was not always a stimulation in shoot nitrogen concentration as significant differences were observed only on three of five occasions. Shoot growth and flowering in *C. vulgaris* were stimulated by nitrogen additions in proportion to application rates during the early years of the experiment. In the low and control treatments applicable to this review, no difference in canopy height was recorded in either nitrogen or drought treatments.

Measurements of soil pH at Budworth Common in June 1996 and June 1998 did not appear to show any significant reduction as a result of nitrogen application. The effect of
elevated nitrogen treatments, plus drought, on the density of *Deschampsia flexuosa* at Budworth Common showed a trend towards an increase of *Deschampsia* in proportion to nitrogen treatment. However, further monitoring at this site by Wilson (unpublished data) has shown that, from 1999 onwards *D. flexuosa* density decreased significantly as the *C. vulgaris* canopy recovered. From the results of this study, the author suggested that increases of nitrogen in excess of 20 kg N ha$^{-1}$ yr$^{-1}$ above ambient inputs may have the ability to disrupt *C. vulgaris*. However, the relatively short duration of this study (3 years) must be taken into account when attempting to extrapolate results from the above statement to other lowland heath sites.

Cawley (2001) demonstrated how resilient *C. vulgaris* appears to be under conditions of elevated nitrogen and short to medium term drought episodes. However, under conditions of severe drought, plant water potentials did appear to fall in proportion to increasing nitrogen supply. Examination of drought sensitivity at Thursley Common showed no effect of nitrogen addition on *C. vulgaris* shoot water potentials in the field (Power et al. 1998a). However, calculation of shoot drying curves showed that *C. vulgaris* plants from control plots lost water significantly more slowly than those plants which received additional nitrogen. Plants exposed to nitrogen additions may therefore become more stressed under drought conditions.

The simulated drought conditions at Budworth Common (May – September 1997) revealed a marked reduction in root mass for droughted plants in all treatment plots. Above ground growth ceased at a much earlier date in droughted plants in comparison to fully watered plants and growth continued in the fully watered plants for several weeks, with greater growth also in high nitrogen plots. It is considered that the implications of such luxuriant growth combined with increased foliar nitrogen content would lead to a pre-deposition to late summer drought, a high risk of winter injury and an increased risk of attack by herbivores and fungal pathogens (Cawley 2001). Indeed, during the third year of this experiment, a spontaneous heather beetle attack occurred. As seen in other biotic stress sensitivity experiments, a distinct preference for enriched nitrogen foliage was shown. Power et al. (1998b) investigated whether nitrogen additions affected heather beetle growth and performance. The relative growth rate of larvae were faster for beetles feeding on shoots from the highest nitrogen addition plots and these larvae grew into significantly larger pupae and adults. A number of other studies have also shown that nitrogen addition increases heather beetle growth and reduces its time to maturity, thereby increasing its damage capabilities and the potential for particularly damaging outbreaks of this insect herbivore (Bardowski 1993, van der Eerden et al. 1991, McNaill et al. 1988, Brunsting and Heil 1985).

**European Studies**

The Danish Heath project is located on several lowland heath sites in Denmark. Nitrogen manipulation studies began at Hjelm Hede, north-west Denmark, in 1993 and involved a range of application rates from 0 – 70 kg N ha$^{-1}$ yr$^{-1}$. The total annual deposition for the area is estimated to be 18 kg N ha$^{-1}$ yr$^{-1}$. An investigation into the response of heathland vegetation to nitrogen addition was carried out by Riis-Nielson (1997). The study involved six sites, representing different stages of succession. Ammonium nitrate was applied six times per annum at rates of 0, 15, 35 and 70 kg N ha$^{-1}$ yr$^{-1}$. No obvious signs of increased (or decreased) growth of any species or increased flowering due to nitrogen fertilisation were found. This absence of growth response could be due to the presence of limiting factors, other than nitrogen. Further investigation on Hjelm Hede has found the site to be limited by phosphorous. It has been suggested that, where phosphorous limits plant growth, heathlands may still be
susceptible to nitrogen deposition, but that they are more likely to be resistant to vegetation changes than nitrogen-limited heathlands. In the summer of 1994, a heather beetle attack occurred at two of the study sites, providing an opportunity to study the response of the heather beetle to nitrogen additions. The largest densities of beetles were found at intermediate nitrogen additions (15 – 35 kg N ha\(^{-1}\) yr\(^{-1}\)). The damage to Galluna vegetation was found to increase with increasing levels of nitrogen (Riis-Nielsen 1997), providing strong support for the link between nitrogen deposition and heather beetle outbreaks.

An investigation into mineralisation and immobilisation rates of nitrogen in heathland soils, using \(^{15}\)N isotope techniques in laboratory incubations of field collected cores, was undertaken by Kristensen and McCarty (1999). Soil samples were taken from under intact and virtually dead *C. vulgaris* vegetation in November 1999. The death of the vegetation had been caused by a naturally occurring heather beetle infestation in the summer of 1994. The heathland had previously been fertilised at rates of 0, 15 or 35 kg NH\(_4\)NO\(_3\) ha\(^{-1}\) yr\(^{-1}\) since 1993. The study found rapid immobilisation of added NH\(_4\) under intact *C. vulgaris* vegetation suggesting that mineralised NH\(_4\) may be re-immobilised in the soil immediately after being released. However, samples taken from under dead *C. vulgaris* vegetation showed that the tight nitrogen cycling in the mineralisation - immobilisation phases was greatly influenced by heather beetle attack, substantially increasing availability of inorganic nitrogen in the soil. These results may point to a unique influence of the *C. vulgaris* vegetation on microbial cycling of nitrogen within the ecosystem to favour low nitrogen availability (Kristensen and McCarty 1999). This study demonstrated that heather beetle infestations have the ability to change the balance of nitrogen cycling within the ecosystem, resulting in substantial increases in net mineralisation in the soil. Consequently, large accumulations of NH\(_4\) occur in soil under *C. vulgaris* vegetation damaged by heather beetle attack and, together, these influences may increase the ability of grasses to gain dominance at heathland sites (Kristensen and McCarty 1999).

Nielsen *et al.* (2000) reported on the biochemical cycling of inorganic and organic compounds in a lowland heath environment (N additions as in Riis-Nielsen 1997) as part of the HEATH project. The results from this investigation show that the ability to retain experimental additions as well as background/naturally deposited nitrogen requires the presence and the integrity of a humified H sub-horizon. As discussed previously in Kristensen and McCarty (1999), as long as the heath functions are undisturbed, elemental cycling is characterised by a strong internal cycle. However, one year after a heather beetle infestation, the mor layer started to decompose, resulting in a large translocation of organic compounds down the soil profile, to the B-horizon. Nutrients were not lost via leaching processes, but were instead re-distributed in the upper soil, with the podzolic B horizon functioning as a nutrient trap to the mor layer. This experiment forms part of an ongoing investigation, and although not yet reported, the re-establishment of *Galluna* vegetation is being monitored.

The Danish HEATH project incorporated an investigation into the influence of ammonium nitrate on root growth and ericoid mycorrhizal colonisation of *C. vulgaris* by Johansson (1999). This experiment was relatively short term as ammonium nitrate was applied at rates of 0, 35 and 50 N ha\(^{-1}\) yr\(^{-1}\) for two years only. However, this work is still of interest in the context of this review since the majority of investigations into the effect of nitrogen of mycorrhizal fungi have been conducted under laboratory conditions. Results showed that ericoid mycorrhizal colonisation of *C. vulgaris* remained unchanged after two years of fertilisation with ammonium nitrate, contrary to expectations based on findings under laboratory conditions, e.g. Moore–Parkhurst & Onglander 1982 and
Stribley & Read 1976. Johansson (1999) concluded that, based on the two year experiment at Hjelm Hede, the effect of nitrogen on the mycorrhizal colonisation of *C. vulgaris* is unlikely to provide an explanation for heather decline under enhanced nitrogen input. An earlier experiment by Johansson (1995) also showed no significant changes to mycorrhizal colonisation. The influence of ammonium nitrate on the composition of the saprotrophic fungi in *C. vulgaris* heathland soil was also investigated by Johansson (2001). No measurable changes in specific composition of saprotrophic soil fungal groups due to nitrogen treatment were apparent. Consequently, the author concluded that a direct impact on the saprotrophic fungal community is unlikely under enhanced nitrogen input, more that changes would result from secondary effects, for example, changes in vegetation, soil and litter quality (Carroll et al. 1999, Power et al. 1998a, Nordin et al. 1993, Nielsen et al. 1987a,b) under sustained deposition of nitrogen (Johansson 2001).

Prins et al. (1991) and Van der Eerden et al. (1990) examined the effect of nitrogen additions on the maintenance of *C. vulgaris* vegetation in The Netherlands, in an area where background atmospheric nitrogen deposition levels were 35-40 kg N ha⁻¹ yr⁻¹. Ammonium sulphate was supplied in 10 annual soil dressings (10, 50, 90 kg N ha⁻¹ yr⁻¹). Soil chemistry was affected by the nitrogen treatments: cation (K⁺, Ca⁺⁺, Mg⁺⁺, Al³⁺) and NH₄⁺ concentrations showing a clear increase with nitrogen dose. The soil became increasingly more acid with increasing ammonium sulphate addition. An investigation of *C. vulgaris* characteristics found there were no significant differences between treatments in plant, root, green shoot or dead wood dry weights between treatments after three years. Levels of nitrogen were, however, significantly higher in *C. vulgaris* green parts from plots receiving the highest nitrogen additions (90 kg ha⁻¹ yr⁻¹).

No vegetation composition changes were found in closed canopy *C. vulgaris* stands. However, where frost damage had occurred prior to commencement of nitrogen additions, there was a vegetative expansion of *Molinia caerulea* and *Deschampsia flexuosa* in response to nitrogen. The number of tillers and biomass of *D. flexuosa* in damaged *C. vulgaris* stands was significantly greater than control plots at all nitrogen application rates; for *M. caerulea* this was the case only at 50 and 90 kg N ha⁻¹ yr⁻¹ additions. In this experiment Bobbink et al. (1992) observed more than a doubling in base cation leaching (Mg, Ca, K) from *C. vulgaris* shoots at the high nitrogen application rates compared to under the control heather vegetation. However, during measurement, no deficiencies of these ions in the shoots of *C. vulgaris* were found and furthermore a significant uptake of NH₄⁺ by *C. vulgaris* shoots was observed.

Investigations by Heil and Diemont (1983), in which a range of low nitrogen application rates (0, 1.75, 7 and 28 kg ha⁻¹ yr⁻¹) were applied as a single dose or as an annual soil dressing for four years, found dramatic floristic changes to heathland in The Netherlands. The floristic composition of the plots was analysed nine years after the cessation of the nitrogen addition regime. The addition of 28 kg N ha⁻¹ yr⁻¹ resulted in a dramatic replacement of *C. vulgaris* by *Festuca ovina*; this was almost complete in plots which had been attacked by heather beetles. No effect was observed in the plots which only received the nitrogen additions on one occasion. An interaction with management was also noted; in older stands of heather (burned 16 years before) no increase in *F. ovina* cover was found in plots which received low nitrogen doses, but the changes in grass-heather dominance were increasingly evident in the more heavily N-dressed plots. In younger plots (1 year old) application of nitrogen, at all doses, had an immediate stimulatory effect on *F. ovina* cover, which was stronger as the amount of nitrogen increased.
The opening up of the heather canopy seems to be a key factor in the transition of heathland to grassland. In plots where there had been considerable heather beetle damage, _F. ovina_ had almost completely replaced _C. vulgaris_; no relationship between heather beetle attack and nitrogen application dose was noted (but see also Brunsting and Heil 1985). In the phosphorus-limited Danish heathlands, the probability of vegetation change to grassland after heather beetle attack is suggested to depend largely on the soil phosphorus-availability (Riis-Nielsen 1997). Heil and Diemont (1983) also showed how additional nitrogen fertilisation could occur from heather beetle infestation. Heather beetle faeces and corpses, during a heavy infestation, were responsible for an additional input in the order of 7 kg N ha\(^{-1}\) in some sites; additionally mineralisation of the _C. vulgaris_ parts, killed by the heather beetle, can also lead to further nitrogen fertilisation.

Van der Eerden et al. (1991) applied, under a partial roof, artificial rain containing ammonium sulphate (2.9, 5.7, 11.3, 22.7, 45.3 and 90.7 kg N ha\(^{-1}\)yr\(^{-1}\) every fortnight to the Asselse Heide lowland dry heath in The Netherlands. Measurements of plant characteristics showed decreases in the root to shoot ratios in both _C. vulgaris_ and _D. flexuosa_ with increasing nitrogen additions. Investigations of litter decomposition rates found those of _C. vulgaris_ and _Molinia caerulea_ to be unchanged by the addition of nitrogen, whilst the decomposition rate of _D. flexuosa_ litter increased at the highest nitrogen doses. These decomposition rates in all species seemed to be limited by the availability of usable carbon in the different litter types. Chemical analysis of the litter types found there to be significant increases in the nitrogen content of _M. caerulea_ leaf litter with increasing addition of nitrogen, whilst no increases were found for _D. flexuosa_ or _C. vulgaris_ leaf litter. Increases in frost sensitivity were also noted in the highest nitrogen addition plots five months after treatment began, but not at seven months (van der Eerden and Dueck 1992). Despite the short duration of this study the results indicate that there could be potential changes in the competitive balance, botanical composition and nutrient cycling patterns in the study heathland. Van Vurren and van der Eerden (1992) also studied the effect of low level nitrogen addition on lowland heath ecosystems. The duration of the study was short (less than two years) and no changes in botanical composition were observed, although smaller changes in soil and plant chemistry were found.

All other whole ecosystem nitrogen manipulations on lowland heathland have involved large additions of nitrogen, at deposition rates ranging from 80 to 200 kg N ha\(^{-1}\)yr\(^{-1}\). Heathland subjected to higher levels of nitrogen addition has shown a variety of responses depending on the form of nitrogen addition (Persson 1981). In liquid fertilised plots, there was a change in the ground cover, from almost exclusively lichen to domination by the bryophyte species _Pohlia nutans_ and _Pleurozium schreberi_. Where nitrogen was applied in a solid form, there were however, decreases of some bryophyte species (_Dicranum polysetum_ and _P. schreberi_). This highlights the problem in interpreting many nitrogen manipulation experiments as the responses observed vary with the experimental procedure employed and the duration of the experiment.

**Summary**

The effect of increased nitrogen deposition on lowland heath ecosystems has been reasonably well studied and a number of experiments involving relatively low additions of nitrogen have been undertaken. The responses of _Calluna vulgaris_, the main component of these ecosystems, have included increased shoot growth, canopy height and density, flowering and litter production, all with nitrogen additions as low as 15.4 kg N ha\(^{-1}\)yr\(^{-1}\). Changes in _C. vulgaris_ shoot chemistry and vulnerability to cold and
drought stresses have also been noted. A number of studies have reported increased damage by heather beetles with increasing nitrogen addition, and decreased larval development times. The ability of heather beetle infestations to bring about changes to the microbial community has also been observed. The opening up of the C. vulgaris canopy through frost, drought or insect damage is considered to be of key importance in the conversion of heathland to grasslands with increased nitrogen addition, with a more open canopy favouring the growth of the grasses Molinia caerulea and Deschampsia flexuosa. The study by Power et al. (1995, 1998a;b, 2001) emphasises the need for long term studies of ecosystem responses to increased rates of nitrogen deposition, as some responses were observed only after a number of years of nitrogen addition. Furthermore, the importance of P availability and habitat management as modifiers of heathland response to nitrogen deposition have been suggested.