2 The effects of nitrogen deposition on the structure and functioning of ecosystems


2.1 INTRODUCTION

Human activities threaten the structure and functioning of natural and semi-natural ecosystems in many ways, and thus also the associated diversity of plant and animal species. One of the main anthropogenic threats in our temperate climate zone is the increased air pollution by both reduced and oxidized nitrogen compounds in the form of NHx and NOy (e.g. Sala et al. 2000; Galloway & Cowling 2002; Bobbink et al. 2010a). Also in the Netherlands it is recognized that high nitrogen deposition is a major limiting factor to maintain or restore a good state of conservation in sensitive natural areas.

As such, nitrogen (N) is not a problem. On the contrary, it is one of the essential building blocks for life on earth. The problem lies in the extent to which this element is added to our environment in reactive form. For centuries, only organic fertilizer or other organic materials were used to increase the agricultural production, while later also guano or ‘Chile saltpeter’ (recovered from bird droppings) were used. This situation changed after the invention of synthetic conversion of the inert molecular nitrogen (N2) into the reactive ammonia by Fritz Haber in 1909 and the industrial scaling of that by Carl Bosch (both got the Nobel Prize). This ‘Haber–Bosch process’ made large-scale fertilizer production possible and its use very much increased after 1920. In the course of the twentieth century, increasing amounts of fertilizer were used to increase agricultural production. Cattle breeding also increasingly intensified as a result. The downside was that more and more reactive nitrogen disappeared from the agricultural system to ground or surface water or through air emissions.

This chapter first covers some basic principles with regard to emission, transport and deposition of nitrogen compounds. This includes the influence of vegetation on the deposition process, including the edge effect. This is followed by a discussion of the main effects of nitrogen deposition that are currently still relevant. These are N–eutrophication, acidification of soil or water and the negative effects of reduced nitrogen. The effects of nitrogen deposition on fauna are then discussed. These effects relate to the invertebrates in particular, as these tend to be highly dependent on the structure and composition of the vegetation. It will be made clear that the relationships in ecosystems are complex. There usually are no simple dose–response relationships. The focus will be on the ecological and chemical processes, so that the significance of the recovery strategies discussed in chapter 3 can be better understood.

The intermezzo directly following this chapter will specifically cover complex processes in damp and wet ecosystems (biogeochemical mechanisms in wet ecosystems). These processes can pose other significant impediments for habitat restoration. This intermezzo explains hydrological recovery measures, which are not primarily directed against the effects of nitrogen.
2.2 EMISSION, TRANSPORT AND DEPOSITION OF NITROGEN COMPOUNDS

The discharge (emission) of air pollution in Western Europe has significantly increased in the course of the twentieth century. Sulphur dioxide \((\text{SO}_2)\) was the main component of air pollution until the late seventies of the last century. After that nitrogen compounds became increasingly important, both relatively and absolutely. Nitrogen oxides \((\text{NO}_x\text{: especially NO}_2\text{ and NO})\) arise mainly from the combustion of fossil fuels in industry, power plants, heating systems and traffic. At the moment, the main source of nitrogen oxides is (freight) traffic. Ammonia gas \((\text{NH}_3)\) is mainly liberated by volatilization from manure and urine during grazing, in the shed or in storage, and previously when the manure was spread on the field. Other sources are industry – where ammonia is liberated during some manufacturing processes or when the \(\text{NO}_x\)-installations malfunction –, car traffic and the storage of effluent.

2.2.1 CHEMICAL CONVERSIONS IN THE ATMOSPHERE

Nitrogen oxides and ammonia end up in the atmosphere after emission. There, these substances undergo chemical reactions under the influence of sunlight and the presence of other materials. The atmospheric conversions can, among other things, lead to the formation of nitrate \((\text{NO}_3^-)\), ammonium \((\text{NH}_4^+)\) and nitric acid \((\text{HNO}_3,\text{ gas phase})\). \(\text{NH}_4^+\) and \(\text{NO}_3^-\) are the dominant N-containing ions in the water–particles in clouds or fog and in precipitation. Ammonia \((\text{NH}_3)\) reacts rapidly with acids, producing ammonium salts. Here, small solid particles (so-called aerosols) are formed, such as \((\text{NH}_4)_2\text{SO}_4\) or \(\text{NH}_4\text{NO}_3\), whereby nitric acid \((\text{HNO}_3)\) and sulphuric acid \((\text{H}_2\text{SO}_4)\) are neutralized by \(\text{NH}_3\). The conversion into aerosols is of importance for the distance across which the substances are transported. In short, nitrogen compounds are found in the atmosphere as gas, ion and aerosol.

2.2.2 TRANSPORT AND DEPOSITION

Once airborne, the emitted gas is carried along by the wind and spread quickly. This can be compared with a plume of smoke from a campfire: the plume is carried along by the wind and dissipated simultaneously. After a few hundred meters, the smoke is no longer visible, while it can still be smelled. Dilution of the concentrations of substances occurs rapidly in the air. All kinds of chemical conversions take place there as well (see above). The various gases and aerosols can thus cover great distances in the atmosphere under the influence of air currents. A complex of different factors determines how far the different components get. Especially important are the emission level, the atmospheric conditions (speed of air currents, turbulence, etc.), the rate of chemical reactions, the deposition rate of the particular compound, and the nature and roughness of the earth’s surface with its vegetation. Eventually all those substances will end up on the earth’s surface. This process is called deposition, and it can occur in various ways (Diagram 2.1).
The direct deposition or absorption of gases or aerosols from the atmosphere to the earth's surface (soil, water or vegetation) is called dry deposition. A measure of the speed of this process is the dry deposition velocity ($V_d$): the higher it is, the faster the gas or the particle is removed from the atmosphere. Thus, the transportation distance of NH$_3$ is short due to the high $V_d$ of this gas, while the transportation distance of the ammonium aerosol is much higher due to its lower $V_d$. A large proportion of the NO$_2$ is discharged by traffic at a low level. However, due to the low deposition velocity of NO$_2$ and the low conversion rates into gases HNO$_3$ and HNO$_2$, both of which have a high deposition velocity, NO$_2$ is nevertheless often transported over long distances. For more background information on the (dry) deposition process, see e.g. Erisman (1992), Asman et al. (1998) and Fowler (2002).

In addition to the direct deposition of gases and particles on the surface, the dry deposition just described, two other processes play a part in the removal of nitrogen from the atmosphere. These are the solution in clouds or rain and subsequent precipitation (wet deposition; see Diagram 2.1) and the deposition of cloud or fog drops directly onto the vegetation or soil (clouds or fog deposition, also called occult deposition). In the Netherlands, the latter process contributes almost nothing (<1–2%) to the total deposition of N compounds from the atmosphere. Wet deposition provides about 25–30% of the total N deposition. The rest is dry deposition (De Haan et al. 2008).

The total nitrogen deposition in the Netherlands increased significantly after 1950 until the end of the eighties of the last century (Diagram 2.2). This was caused by increased intensive stock farming and the use of fossil fuels. From 1993, a decrease (30–40 %) in the deposition of reduced N (ammonia and ammonium) was realised through various measures. From 2003 up to the present the values have remained roughly constant. The deposition of oxidized N (nitrogen oxide)
also increased after 1945, but levelled off earlier than the deposition of reduced N. After 1980 to 1985 a very gradual decline has been observed. For about three to four decades reduced N has been the predominant form (> 75%) of nitrogen deposition in Dutch nature areas (De Haan et al. 2008).

At present, more than half of the nitrogen deposition in the Netherlands comes from domestic sources, the rest comes from abroad or from "natural" sources (Diagram 2.3). Agriculture is the economic sector, which by far contributes the most to nitrogen deposition from the Netherlands (46% in 2004).
Diagram 2.3 Contribution (%) of the various sources to the total nitrogen deposition in the Netherlands in 2004 (From De Haan et al. 2008).

Afkomstig uit Nederland = from the Netherlands
Landbouw = agriculture
Overig = other
Afkomstig uit buitenland = from abroad
Natuurlijke achtergrond = natural background

The deposition of ammonia from an agricultural source is high in the vicinity of that source in comparison with the deposition at a greater distance from that source. Starting from a point source of ammonia at a 3 m height (for example, a shed), about 20% of the released ammonia comes down within a distance of one kilometre from the source. On this scale, it almost exclusively concerns dry deposition of ammonia. Wet deposition only plays a significant part after 10 kilometres. After a 100 km transport about 60% of the released ammonia has been deposited. There is, however, also transport over very long distance: after a 1,000 km about 20% of the original ammonia is still in the atmosphere in some form (e.g. Kros et al. 2008).

Due to the spatial distribution of the sources and the various transmission and conversion processes in the atmosphere, the deposition of N-compounds is not the same everywhere (Diagram 2.4). Even in a small country like the Netherlands there are major differences: for example, the total deposition of NO$_x$ (the sum of dry and wet deposition of NO + NO$_2$ + HNO$_3$) is clearly higher in urban areas (including in the west of the country), while the total deposition of NH$_x$ (the sum of dry and wet deposition of NH$_4^+$ en NH$_3$) is higher in rural areas, where the highest values are found in the Peel region, the Gelderland Valley, Twente and the Achterhoek.
2.2.3 THE INFLUENCE OF VEGETATION ON THE DEPOSITION PROCESS

The nature of the vegetation also plays a part in the dry air deposition. In general, a "rougher" vegetation has a more filtering effect. The rougher surface provides more turbulence in the air just above the vegetation. Due to this turbulence, the gases or aerosols travel a more winding road as it were, instead of a straight road as is the case above a smooth surface. As a result, the particles are found above the interface of the vegetation and the air for a longer period of time, and with that the chance of deposition or absorption, thus dry deposition, increases. The above example relates to both the dry deposition of NH$_x$ as that of NO$_x$ (and SO$_x$).

In general, the higher a vegetation is, the more dry deposition takes place. The aerodynamic roughness and with that the filtering effect and dry deposition velocity increase in the following order: open water / bare soil < low grassland < high grassland < heath < shrubs < broad-leaved forest < pine forest. In short, forests have greater aerodynamic roughness than low vegetation, so that there is a higher dry deposition of nitrogen than when the same area would have been covered by grassland or heath land. In other words, in this way, with equal concentrations of NH$_x$ and NO$_x$, a lot of extra N can be found in forests. Nevertheless, the dry deposition within one physiognomic group, such as forests, is not at all always the same. The fact is that the dry deposition is not only determined by the height of the vegetation, but also influenced by other characteristics of the forest that affect the aerodynamic roughness. Examples include the structure of the crowns (homogeneous or not), tree density, tree species, differences in leaf characteristics or the total leaf area (Van Ek & Draaijers 1991, Draaijers 1993, Wuyts et al. 2008b).
Although it was believed until the nineties of the last century that low vegetation, such as grassland, would barely capture extra dry deposition compared to bare soil or open water, field research in several countries, including the Netherlands, has shown that dry deposition in low vegetations is not negligible. With increasing Leaf Area Index (LAI), which is to say, the total leaf area of the vegetation per unit of soil surface, the dry deposition of S- and N-compounds in grassland significantly increases (Heil et al. 1988; Bobbink et al. 1990). The increase in dry deposition occurred at LAI values above 1.5–2, while in highly productive grasslands with an LAI of 4–6 the dry deposition is almost as high as in some forests. In fact, therefore, the larger leaf area low vegetation has, the more air turbulence and filtration occurs, resulting in a greater dry deposition of substances from the atmosphere. A portion of the nitrogen compounds deposited from the air is immediately absorbed by plants above ground through the leaves, particularly in the nutrient-poor to moderate nutrient-rich conditions.

EDGE EFFECT

Research in both coniferous and broad-leaved forests in the 1980s showed that transitions in the landscape, such as from low vegetation (e.g. grassland or heathland) to forest, also greatly affect the dry deposition process of air pollutants (e.g. Ivens 1990; Draaijers 1993). The dry N deposition in an approximately 10–20 m wide woodland fringe is significantly higher (on average 1.5 x) than that in the centre of the forest and it decreased exponentially to the regular deposition values in the centre of the forest. The dry deposition is measurably increased in an edge zone, which is comprised of the first five edge heights. This enhanced deposition of N- and S-compounds was most prominently found in woodland fringes that were exposed to the prevailing wind directions (Draaijers 1993). Recently, a similar study was conducted in Flanders. It showed that the nitrogen deposition in woodland fringe zones is 0.5 to almost 4 times higher than that in the centre of the forest (median values: 1.5 for NH$_4$ and 1.6 for NO$_3$) (De Schrijver et al. 2007; Wuyts et al. 2008a).

The zone in which elevated levels were detected was between 15 to over 100 metres wide (median value: 50 m), within which most was captured in the first section. Apart from that, an increased N-capture also takes place in the short vegetation right next to the edge of the forest (Wuyts et al. 2009). Because forests in the Netherlands are often very fragmented and small, at least half of the forests can be considered as woodland fringe zones with enhanced deposition (Draaijers 1993). Moreover, in almost all N-deposition models, including those for the PAS (AERIUS), transitions between forest and low vegetation are not taken into account. After all, fixed parameters for each vegetation class (e.g. forest or heath) are used for calculations. Because of the edge effect the atmospheric nitrogen deposition on forests is therefore often underestimated (Draaijers 1993).

In addition, the following aspects were quantified in the recent Flemish research (Wuyts 2009):

- It makes a big difference whether there is a sharp transition from low vegetation to forest or a woodland fringe that is gradually increasing in height (in the form of a zone of saplings or a gradual edge vegetation): the additional deposition in the woodland fringe is significantly greater when there is a sharp transition compared to when there is a gradual transition, and the zone in which the edge effect occurs is wider when there is a sharp transition compared to when there is a gradual one (see also Table 3 in Wuyts et al. 2009).
- The width of the zone in which the edge effect occurs is smaller when there is a dense forest
compared to when there is sparse forest, but the extent of the edge effect (i.e. the amount of additional capture in the edge zone) is larger in the case of a dense coniferous forest compared to in a sparse coniferous forest (Chapter 6 in Wuyts 2009).

When taking management and restoration measures in the context of the PAS, this ‘deposition behaviour’ can possibly be taken into account. To reduce the capture of nitrogen, the following measures concerning structure are imaginable:

• to capture nitrogen outside sensitive habitats by maintaining or developing dense, high forests (preferably coniferous forests) with a sharp woodland fringe in the zone between the nitrogen sources and sensitive habitats (the forest then serves as a buffer zone);
• to develop edge and mantle vegetation as a gradual transition between low vegetation and the woodland fringe zones that need to be protected (this reduces deposition in the wood fringe zone);
• if a gradual transition cannot be realized, then concentrate the quality improvement of forests on areas that are not part of the woodland fringe zone, or – if the woodland fringe zone is valuable – thin this zone so that relatively little additional nitrogen is captured in this zone.

2.3 Different effects of nitrogen deposition

Six different effects of nitrogen deposition can be distinguished (see Chapter 1). The current chapter will elaborate on the three main effects. These are eutrophication by gradual increase of N-availability, acidification of soil and water and the negative effects of the increased availability of reduced N (ammonium).

2.3.1 N–eutrophication

The increased uptake of nitrogen by the vegetation usually causes an increase in biomass production of plant parts aboveground in particular, seeing that the productivity of many terrestrial ecosystems in areas with a temperate climate, such as in Western Europe, is in principle limited by nitrogen (e.g. Vitousek & Howarth 1991; LeBauer & Treseder 2008). Due to this increase in productivity the plant litter production is also increased, and gradually also the release of nitrogen compounds from organic material (Diagram 2.5). This process is called mineralization. Because the nitrogen cycle is closed in many natural situations of our climate zone, this means that the nitrogen inventory in the system is ever increasing due to N-deposition, and so making more nitrogen available due to the higher mineralization (Aerts & Bobbink 1999).

Only after a prolonged high nitrogen supply is there increased leaching from the upper soil layers to the groundwater. Also, by this, various ecosystems will no longer have become nitrogen–limited but phosphorus–limited. Furthermore, the succession accelerates due to the increased nitrogen availability, in particular in systems that are still developing. In this way, accelerated tree growth can occur, such as a strong increase of birch in peat moors, but also more and rapid shrubs formation in the dry dunes.
SHIFTs IN COMPETITION

In time, the increase in the availability of nitrogen will cause shifts in the competition between plant species and thus to changes in the dominance of species and the species composition of the vegetation. Nitrogen–loving, fast–growing plant species thus gradually displace the characteristic, less competitive species and will eventually dominate the vegetation. Recently it has been shown experimentally that the reduced light penetration in grassland vegetation is the determining factor (Hautier et al. 2009). A large part of the species in semi–natural and natural ecosystems is adapted to a low nitrogen availability in soil ( Ellenberg 1988). As a result thereof, the wealth of plant species will in the long term decline in nutrient–poor to moderately nutrient–rich systems. Low–growing herbs, such as rosette plants and short–lived species, nitrogen–fixing plants such as papilionaceous flowers, species with traditionally small populations and lichens will decrease, whereas nitrogen–loving species, including various gramineae, will dominate (e.g. Bobbink et al. 1998, Clark et al. 2007). Examples of species which make up grassy or rugged ecosystems are Wavy Hair–grass ( Deschampsia flexuosa) and Purple Moor Grass ( Molinia caerulea) in heathlands, Heath False Brome ( Brachypodium pinnatum) in calcareous grasslands, Bushgrass ( Calamagrostis epigejos) and European beachgrass ( Ammophila arenaria) in the dunes and blackberries (including Rubus fruticosus aggrr ). Wavy Hair–grass and European elderberry ( Sambucus nigra) in forests (Diagram 2.6 and 2.7) (e.g. Dise et al. 2011). In short, rare species are becoming increasingly rare and common species more common. The vegetation composition also becomes more homogeneous (‘homogenisation’), because the micro variability in light penetration and nutrient concentrations (nitrate and ammonium) are greatly reduced by the above
processes. This also usually means a decrease in habitat specific species, and a consequent lower local quality of the habitat type.

Diagram 2.6 Image of calcareous grassland vegetation without an extra N-donation (left) and after a 3 years’ treatment with 100 kg N ha\(^{-1}\) yr\(^{-1}\) (right) (pictures: R. Bobbink). Through N-eutrophication, the growth of the grass Heath False Brome (Brachypodium pinnatum) increased very dramatically under the mowing management of that time, causing the disappearance of many low herbs from the vegetation (Bobbink 1991).
Diagram 2.7 Cover of Rubus fruticosus aggr. in Swiss forest observation plots in relation to the total nitrogen deposition: the cover is usually substantially higher when the nitrogen deposition is higher than 20–25 kg N per ha per year (from Flückiger & Braun 2004).

In addition to the effects on higher plants, an excessive supply of nitrogen also causes a deterioration of fungi, in particular of the ectomycorrhizal species (Arnold 1991). In the Netherlands, these are mainly forest mushrooms that live in symbiosis with the roots of trees. The ectomycorrhizas are, inter alia, of great importance for the nutrient uptake of trees. Many species of this group have become rare or have almost disappeared from our forests. Also, the charge of ectomycorrhizal species on tree roots decreases due to increasing nitrogen supplies. This potentially has adverse effects on the growth and development of the trees themselves (Bobbink et al. 2003). Another effect that occurs is the change in microclimate. Because of earlier plant growth the soil warms up more slowly in the spring, slowing down the development of, for example, butterflies, which made it through winter as an egg or caterpillar. This can lead to a mismatch with the vegetation growth (food for caterpillars), to lower survival and smaller populations (Wallis de Vries & Van Swaay 2006). See paragraph 2.4.1.

DECREASE IN SPECIES RICHNESS

The increase in the availability of nitrogen can not only lead to changes in the species composition of vegetation, but can often also cause a decrease in species richness. For example, a recent comparison of plant species with various abiotic factors in dry low-nutrient grasslands (habitat type 6230) in nine countries across Europe revealed that species richness is mainly related to the total N deposition, and that this relationship is primarily negative: as N deposition increases, the number of species decreases (Figure 2.8; Stevens et al. 2010). Dorland & Van Loon 2011 analyse the data in this figure in more detail. They propose a sigmoid curve, in which an average of 20 species in cases of low deposition falls to an average of 11 species in cases of high deposition. This decrease mainly takes place between 12 and 29 kg N/ha/yr (after which the number of species stabilises). The extinct species are primarily those which are characteristic of a particular habitat type, such that the vegetation remaining in cases of high deposition often no longer meets the definition of that habitat type. This means that loss of quality may ultimately also lead to surface loss. Habitat types that are naturally acidic, are often characterised by species that are highly resistant to acidification and toxicity caused by ammonium and aluminium, and these types are therefore particularly sensitive to the long-term effects of eutrophication, since the nitrogen availability was originally very low.
Critical loads reflect the sensitivity of ecosystems: the lower the critical load, the more sensitive the system. In section 1.2.1 explains how critical loads come about. In many areas of the Netherlands, the current nitrogen deposition exceeds the critical load of the existing habitat type, this means that the critical load has been exceeded (also known as 'exceedance'). The figure above indicates the likely effects on the species richness when the critical load is exceeded. Figure 2.8 shows this for an individual habitat type. As mentioned above, the decrease in species occurs at around 12 kg N/ha/yr, which corresponds with the critical load established for this habitat type (model outcome 11.6 kg N/ha/yr, consistent with the empirical range of 10–15 kg N/ha/yr; see recovery strategy H6230 in Part II).

Figure 2.8 The relationship between the number of plant species in low-nutrient grasslands (Violion Caninae) as they appear across Europe and the N deposition. The negative relationship observed is highly significant (Stevens et al. 2010).
There is also experimental evidence that the species richness in nature reserves will actually reduce as the excess of the critical loads increases. This can be seen in figure 2.9, in which a significant negative correlation was found between the exceedance of critical loads and the species richness ratio in experiments with the addition of N in European nature reserves with a variety of non-forest vegetation (Bobbink & Hettelingh 2011). The excess is calculated as the sum of the experimental N-dose plus the background deposition minus the critical load. Values under 1 indicate that the species richness is lower in cases of excess than in the control study. So 0.75 means that species richness has declined by 25%.

![Figure 2.9](image.png)

*Figure 2.9 Overview of the relationship between plant species richness and excessive (in kg N/ha/yr) critical loads. Each point is the average result of an N-addition experiment in grasslands, montane heath and subarctic and subalpine (heath) vegetation, where the species richness in the N-treatment is divided by those in the control plots (species richness ratio). (Bobbink et al. 2010c).*

**DISTURBED NITROGEN CYCLE AND NITROGEN LEACHING**

In addition to the changes described above in the competitive position, the speed of the nitrogen cycle in the system gradually increases through nitrogen eutrophication (Aerts & Bobbink 1999). The vegetation’s biomass production is higher and includes more litter production both above and below ground, often with higher nitrogen concentrations. This initially serves to increase the rate of degradation of the organic material (mineralisation). However, there is also evidence that the decomposition of litter in fact slows down in the long term, due to increased N concentrations and depending on which stage the formation of humus has reached (Berg & Matzner 1997; Hagedoorn et al. 2003). Mechanisms for this are provided in Janssens et al. 2010. At the same time, the immobilisation of ammonium and nitrate in several systems decreases through heterotrophic micro-organisms, eventually causing the excess of nitrogen to be made available
more quickly for the vegetation (Tietema et al. 1993; Nadelhoffer et al. 2004). This has also been found in the case of dune ecosystems, where the phenomenon was most apparent in acidic soils (Kooijman & Besse 2002, Kooijman et al. 2009).

Changes in the vegetation composition may in themselves also result in additional acceleration of the nitrogen cycle, due, for example, to the fact that the litter from the now more dominant species contains higher levels of nitrogen and thus breaks down more easily (Aerts & Chapin 2000). In the case of a consistently high nitrogen deposition, plant growth is no longer limited by nitrogen after a certain point, but rather by another element (phosphorous, potassium or magnesium), or for example, a lack of water (Aerts & Bobbink 1999). In such cases, there is no additional growth due to an excessive supply of nitrogen – although a part of the additional nitrogen will be absorbed by the vegetation. The latter leads to even higher nitrogen concentrations in the vegetation which affect the amount of nitrogen in the litter and the mineralisation of nitrogen.

The aforementioned processes cause the C/N ratio of the soil’s top layer to gradually decrease.

The continuous accumulation of nitrogen, increased speed of the nitrogen cycle and saturation of the ecosystem with nitrogen steadily increase the risk of inorganic nitrogen leaching into the (shallow) groundwater. A system like this is referred to as being saturated with nitrogen. This term is used mainly for forests and forests saturated with nitrogen characteristically show reduced levels of the C/N ratio from the organic horizon, increased nitrate leaching, increased emission of N₂O and the termination of the growth stimulation by additional nitrogen. In some cases, a decline in tree growth may also occur. In terrestrial systems, nitrogen almost always gets washed away in the form of nitrate, since ammonium in the soil is not very mobile, and only a very limited amount disappears into the groundwater. It is only in wet systems, including peatlands, that ammonium leaching to the groundwater can also be of quantitative importance (Kros et al. 2008).

In the deciduous and coniferous forests of Europe, nitrate leaching into the groundwater is strongly related to the total nitrogen deposition that enters the forest (see Dise & Wright 1995; De Vries et al. 2007; Dise et al. 2009). In cases of nitrogen deposition below 8–10 kg N/ha/yr, almost no nitrate leaches into the groundwater in forests. Furthermore, increased nitrogen deposition causes the leaching to increase significantly. The identified correlation is clear, although a greatly increased supply and saturation means the variation in nitrogen leaching is quite large (Figure 2.10). This is primarily related to the C/N ratio of the topsoil and the significant differences in climate (temperature, humidity) in the gradient studied in Europe.

Increased nitrogen deposition can increase the amount of nitrogen (in the form of nitrate) that enters the groundwater system and thus also the outgoing surface water or groundwater–fed vegetation. During this transport process, nitrate can seep into pyrite layers by way of denitrification. Unfortunately, this causes the sulphide to be converted into sulphate, which can have serious consequences for these wet ecosystems, following transportation by groundwater–fed systems (for details on this process, see the Intermezzo following this chapter).
Figure 2.10  The leaching of nitrogen compounds into the groundwater under NW European forests in relation to the supply of nitrogen from the atmosphere (Dise & Wright 1995).

The altered nitrogen chemistry of the vegetation can also have serious consequences for herbivores and thus the rest of the food chain in the ecosystem (see section 2.3.5). In addition to the increased nitrogen concentrations, the proportions of this element in relation to other nutrients (especially phosphorus, magnesium and/or potassium) are disrupted, and this nutrient imbalance can, in turn, have serious consequences for the growth and development of plants and trees (see, for example, Nihlgard 1985; Roelofs et al. 1985). This phenomenon is exacerbated in situations where soil acidification occurs, with cations such as magnesium and potassium leaching at an accelerated pace and the relationship between nitrogen and cations can become even more unbalanced (see section 2.2.2). This process was probably one of the reasons that a decline in vitality was observed among various species in the Netherlands in the 1980s (see, for example Van Dijk 1993). Very strong reductions in the S deposition – and to a lesser extent, in the N deposition – have put a stop to this decline in vitality, and some species have even improved again.

2.3.2 ACIDIFICATION

In addition to eutrophication, acidification of the soil or water is one of the main effects of the atmospheric deposition of N compounds. Understanding the processes that lead to soil acidification is thus essential when implementing effective restorative measures to combat the effects of N deposition. A significant proportion of the negative effects of N deposition on biodiversity is due to soil acidification, particularly in the case of ecosystems that were originally weakly buffered (pH 4.5–6.5) (see, for example Bobbink et al. 1998).
BUFFERING CAPACITY OF THE SOIL

A soil bearing vegetation does not only consist of an aqueous solution (soil moisture), but also a solid phase (mineral soil, organic matter). Micro-organisms, soil fauna and underground plant components are also present – in short, a complex system. It is therefore insufficient to simply measure the pH of the soil moisture in order to determine acidification, as shown by the following.

As an example of what can happen during the soil acidification process, a hydrochloric acid solution is slowly added to a calcareous soil (CaCO) (Figure 2.11). It appears that the pH in the water, which is collected at the bottom of the soil, remains between 7 and 8 for quite some time. The soil water does not get more acidic initially. The fact that the pH does not drop, in spite of the addition of acid, is because buffer reactions – such as lime dissolving – may occur. As such, a better definition of soil acidification is the reduction in the buffer capacity – also known as the acid neutralising capacity (ANC) of the soil. During the process, the ground loses a pH–buffering substance (see below in reaction 1) which is only available in finite amounts. Once that is nearly completely finished, the pH will fall.

![Figure 2.11 The schematic course of the acidity in a well-drained calcareous soil column with the continuous addition of a strong acid (source: Ulrich 1981).](image)

The buffering capacity of the soil can be reduced both by natural processes and by the deposition of acidifying pollutants (nitrogen and sulphur). The deposition of NH₃ also contributes to this process through nitrification in which acid (H⁺) is produced (see below). Acid–consuming processes occur in the soil which in turn increases the buffer capacity. This process is also called alkalisation, as a hydroxide ion (OH⁻) or bicarbonate (HCO₃⁻) is released. Denitrification and sulphate reduction are two of the most important soil processes that can consume acid. For details about these processes, see the Intermezzo. These processes ensure that the pH is usually...
high under reduced conditions in wet soils and remains relatively high in cases of high deposition.

**BUFFERING MECHANISMS AND SOIL ACIDIFICATION**

There are a number of mechanisms that can be used to buffer the supply of acidifying substances to soils. The way in which this buffering takes place depends on the base material (the type of soil), and whether or not there is an inflow of ground water (see below). If a lime-rich, dry soil with a neutral pH value (pH = 7) is continuously irrigated with an acid solution, the following pH-changes will occur in sequence due to various buffer mechanisms (Figure 2.11). A detailed description of this is provided in Ulrich (1981).

1) **Carbonate erosion**: in calcareous soils (pH > 6.8), buffering takes place through the reaction of the acid with the lime that is present (CaCO₃ – solid phase):

\[
\text{CaCO}_3 + \text{H}^+ \rightarrow \text{Ca}^{2+} + \text{HCO}_3^- \quad (1)
\]

During this process, calcium and bicarbonate dissolve which leaches ions into the groundwater. The original concentration of H⁺ in the soil does not change initially, such that the pH remains constant. Compared with other buffering mechanisms, the reaction of acid with lime is rather quick. If the calcium content is reduced to less than about 0.3%, then the buffering capacity almost disappears through carbonate erosion and the pH suddenly drops quickly (De Vries et al. 1994). Measurement data and model simulations suggest that such calcium levels can reduce the pH in the topsoil (the upper 10cm) of calcareous dune soils from approximately 6.5 to 3.0 within a few decades. The low erosion rate and almost negligible availability of exchangeable cations and Al hydroxides cause the rapid decline in pH predicted in these soils. In other soils, however, the decrease in pH is slowed down by mechanisms which are discussed below.

2) One buffer mechanism that is present in lime-free (or decalcified soil) with a pH range between 4.2 and 6.5 is that of the cation exchange through the soil’s absorption complex (Figure 2.12). This complex is composed of clay minerals and/or organic components that are negatively charged on the outside, which causes cations (Ca²⁺, Mg²⁺, K⁺, Na⁺) to this complex to be weakly adsorbed. When additional H⁺ comes into the ground, the hydrogen ions can displace the cations in the complex, which causes these cations to end up in the soil solution. The hydrogen ions themselves are then adsorbed on the complex, and no longer dissolve meaning the pH does not change.

![Figure 2.12 Schematic representation of the acid buffering by cation exchange (changed according to De Graaf et al. 1994).](image-url)
Cation exchange is a fast-running buffer process, but the capacity is quite limited. The capacity is gradually reduced through displacement by hydrogen ions. The term 'base saturation' is normally used in such cases to indicate what percentage of the soil's adsorption complex is occupied by so-called base cations (Ca$^{2+}$, Mg$^{2+}$, K$^+$, Na$^+$). The term 'basic' is used here because the respective cations are derived from strong hydroxides, also known as bases.

3) A reaction which is much slower but almost always provides a very large buffer capacity is the weathering of silicate minerals. This reaction occurs in lime-free soils (pH < 6.5). Primary silicate minerals dissolve to produce secondary silicates. One example is the erosion of alkali feldspar:

$$2 \text{KAlSi}_3\text{O}_8 + 2 \text{H}^+ + 9 \text{H}_2\text{O} \rightarrow 2 \text{K}^+ + \text{Al}_2\text{Si}_2\text{O}_5(\text{OH})_4 + 4 \text{H}_4\text{SiO}_4$$

This process is generally very slow. This low speed means this mechanism contributes to the increased supply of acidifying deposition but only slightly contributes to the actual buffering in the soil. Ecologically speaking, this is not of very important in the short term (years, decades). However, this process is quite important in soils where the cation exchange plays an even smaller role.

4) The next buffer mechanism in lime-free, acid soils (pH < 4.5) is the weathering of the aluminium contained in the soil. We refer to the aluminium buffer range in which the following reaction occurs:

$$\text{Al(OH)}_3 + 3 \text{H}^+ \rightarrow \text{Al}^{3+} + 3 \text{H}_2\text{O}$$

When this reaction is triggered, an increasing amount of Al$^{3+}$ enters the soil solution, whereas Al was previously almost exclusively present in its non-dissolved form in the soil. In the same way as H$^+$, Al$^{3+}$ can also be bound to the soil complex, but this process cannot prevent an increase in free Al$^{3+}$. It is important to note that (dissolved) Al$^{3+}$ is toxic for many plant and animal species. If high levels of Al$^{3+}$ are found in the soil moisture, this means that the buffer capacity of the soil has already been consumed to a large extent (Figure 2.11). At this point, it is useful to mention the iron buffer range (not shown in Figure 2.11). If the pH levels are < 3.8, amorphous iron oxides dissolve in case of acid buffering reactions in the presence of dissolved organic matter, while if pH values are < 3.0, iron plays an increasingly dominant role in soil buffering and a (very) high amount of Fe$^{3+}$ dissolves (Verstraten et al. 1989). This last process (pH < 3.0) occurs seldom in practice in the Netherlands, but was prominent, for example, in the 1980s/1990s in the extremely overburdened 'black triangle' of Europe.

5) In systems with bicarbonate in the soil water – caused, for example, by regional seepage – buffering by bicarbonate may occur:

$$\text{HCO}_3^- + \text{H}^+ \rightarrow \text{H}_2\text{CO}_3$$

Buffering by bicarbonate is the most important buffer mechanism in surface water, but is relatively insignificant for the majority of terrestrial situations. The amount of bicarbonate in the soil water is generally quite low and so the capacity of this buffering is also low compared to the
previous four buffering mechanisms unless there is a regular supply of bicarbonate through groundwater seepage or flooding of the surface water occurs. The extraction of groundwater and the regulation of the surface water has often indirectly caused acidification through the loss of seepage or flooding. Besides bicarbonate, calcium (or other base cations) is also supplied through seepage or surface water, which allows the base saturation to be recharged through the aforementioned cation exchange. This is discussed in the next section.

SENSITIVITY TO ACIDIFICATION: A WORLD OF DIFFERENCE

It should be made clear that the precise course of the reduction in buffer capacity (acidification of the soil) and the effects of this on the pH of the soil moisture are highly dependent on the soil material, and its position in the landscape. Buffering is not present everywhere in the landscape in equal measure. We discuss the situation in the Dutch countryside in sequence, going from high to low levels.

In locations where permanent infiltration (downward movement of groundwater) occurs, the pH depends on the weatherability of the mineral fraction of the soil. The pH levels in lime-free cover–sand areas are low (5.0 or less) and buffering primarily takes place through cation exchange or aluminium buffering. Higher pH values (weak acid to acid) may occur in loamy soils. These types of soils are found in areas where loess, boulder clay or loamy cover–sand is on the ground surface or close beneath it. Buffering takes place here through cation exchange.

In moist to wet soils where seepage or flooding occurs (periodically), this water flow is usually an important supply of buffer substances (cations, bicarbonate), which can greatly increase the buffering through cation exchange with the adsorption complex. Regular flooding with surface water that is rich in sludge and alkali causes the soil to have a soil adsorption complex with high capacity that is periodically saturated with bases. Outside the inundation period, pH levels are in the weak acidic range, because the base saturation is reduced due to the exchange of $H^+$ for base cations. If the periodic supply lapses or the intervening periods become longer, the base saturation will decline even further and reduce the cation exchange. The pH is subsequently buffered to a lower level.

The presence of bicarbonate–rich groundwater in the root zone buffers the pH level into the neutral to weakly acidic range. Groundwater is usually rich in bicarbonates due to the fact that it has passed through calcareous layers as it flowed to seepage areas (see equation 1). This means it is enriched with cations, namely $Ca^{2+}$, such that the adsorption complex becomes saturated with bases in periods of seepage or capillary rise. In periods where no seepage occurs, the available bicarbonate gets used and the cation exchange with the adsorption complex takes over the buffering effect. Local high–level seepage from canals, water supply ditches or polders is often rich in bicarbonate and cations and is therefore similar to 'natural' bicarbonate–rich groundwater. In such cases, the ionic composition is different, which is evident from the increased levels of $Cl^-$, $Na^+$ and $K^+$, for example.
Local groundwater systems with bicarbonate- and calcium-rich groundwater also arise in areas where the soil contains some calcareous material at a certain depth. Areas that are supplied by the local base-rich water – such as those described in the above situation with regional seepage – are buffered in the neutral to weakly acidic range by bicarbonate and cation exchange. Places where the soil contains calcareous material at a certain depth appear in areas such as South Limburg, the central and western parts of North Brabant, and in the Achterhoek, Twente and Salland. If lime is lacking in the flow-through, the pH in local seepage areas will be buffered at a (much) lower level.

All this means soils are very sensitive to acidification in some areas, and in other areas, hardly at all. A quantification of the sensitivity to acidification based on the above considerations is provided by De Vries et al. (1989). This analysis shows that, in the Netherlands, the Pleistocene sandy soils in the centre, south and east of the country and the dunes along the coast are particularly between susceptible and very susceptible to accelerated soil acidification through atmospheric deposition (Figure 2.13).

Figure 2.13 Overview of acidification of sensitive soils in the Netherlands. The indicated dark sections are sensitive to soil acidification through atmospheric deposition (source De Vries et al. 1989).

If you compare this map with the deposition in the Netherlands, you immediately notice that the deposition of NH₃ is highest in these areas which are sensitive to acidification. Furthermore, this national scale hardly shows where soils are being buffered by the supply of groundwater and are therefore (much) less sensitive to soil acidification.
EFFECTS OF SOIL ACIDIFICATION: A COMPLEX OF FACTORS

During soil acidification, all kinds of conversions take place in the soil, in which all kinds of cations can be dissolved alongside the decrease in the buffer capacity (ANC). Because annual rainfall in the Netherlands exceeds evaporation, a downward transport of water occurs on average over the year. These water flows allow these cations to leach into deeper layers or to the groundwater. Due to the electrical neutrality in the downward transport of cations, mobile anions such as bicarbonate (HCO$_3^-$) and chloride (Cl$^-$) (in neutral soils) or SO$_4^{2-}$, NO$_3^-$ or organic acid residues may wash out (in acidic soils). Soil acidification can seriously affect the nature of an ecosystem and thus its biodiversity: pH levels can decrease significantly, base cation shortages may occur and an excess toxic metals, especially Al$_3^+$ can be released (Figure 2.14). The decrease in pH levels (<4.5) may increasingly inhibit the nitrification, increasing the ammonium–nitrate ratio and, finally, the rate of degradation of organic material (decomposition) can be greatly reduced which causes litter accumulation in acidified ecosystems to be very common. Because several species cannot tolerate the combination of a low pH and high concentrations of NH$_4^+$ and released Al$_3^+$ acidification almost always leads to a loss of species. A detailed overview of the effects of acidification is provided in De Vries 2008.

![Figure 2.14 Overview of factors that (can) change in the soil due to acidification (according to Bobbink & Lamers 1999).](image)

ACIDIFICATION OF SURFACE WATERS

Surface waters with low alkalinity have a low buffering capacity. Deposition of N and S will therefore respectively lead directly or indirectly to acidification. Additional ammonium will be nitrified in these waters (at pH > 4.0). During this process, H$^+$ ions will be formed which cause the pH levels to drop. Experimental studies have shown that a two–year treatment 19 kg N/ha/yr may already lead to major changes (Schuurkes et al. 1987). When the pH drops below 5 as a result of these acidification processes, acidic–intolerant freshwater species will disappear (Arts et al.)
A proportion of the species that are characteristic of weakly buffered and very weakly buffered fens, such as Shoreweed (*Littorella uniflora*), can still remain below a pH of 5, but submerged peat moss may grow over these freshwater plants. Besides the excessive growth of peat mosses, a (temporary) proliferation of Bulbous Rush (*Juncus bulbosus*) also often occurs, that specifically responds to ammonium (and not to the acidifying effect of S; Schuurkes et al. 1987). Under these circumstances, peat mosses and bulbous rush make the most of the high availability of nitrogen and carbon and can therefore quickly build up biomass and become very dominant (Schuurkes et al. 1986). As such, all characteristic plants gradually disappear from acidified fens due to changes in water chemistry and the massive growth of bulbous rush and toothed sphagnum.

**ACIDIFICATION AND FAUNA**

Besides the effects on plants, acidity of the soil can also affect the fauna (see also section 2.4). Soil acidification causes increased levels of cations (Ca, K, Mg) to leach from the upper soil layer to deeper layers. Due mainly to the shortage of Ca$^{2+}$, snails, woodlice and millipedes (all with a calcium-dominated exoskeleton) disappear into strongly acidified soils. In those circumstances, insects provide too little calcium. This causes songbird eggshells—which depend on these prey—to become thinner and their breeding success to decrease significantly, especially in areas where no other sources of calcium are available. This phenomenon has been clearly demonstrated for the great tit, but is probably also the case for other birds in these acidified ecosystems (Graveland et al. 1994).

In the case of sparrowhawks (*Accipiter nisus*) in nutrient-poor forests, it was found that a mineral deficiency in oak leaves was leading to the absence of a specific protein that can transport and store vitamin B2 in caterpillars. Although these effects were not observed in the caterpillars that eat the leaves and the great tits (*Parus major*) (with relatively short lives), which mainly feed on these caterpillars, a vitamin B2 deficiency was found to occur in the long-living sparrowhawk. This resulted in a sharp decrease in breast muscle and low levels of vitamin B2 in their eggs, which was in turn linked to fatal embryonic abnormalities (Van den Burg 2000). This may also play a role for other long-living species.

**2.3.3 THE NEGATIVE EFFECTS OF REDUCED NITROGEN**

Nitrate and ammonium are the inorganic forms of nitrogen which occur in soil and water, and which may be used as a source of nitrogen by plants. A wide range of ratios of nitrate and ammonium occur in semi-natural and natural ecosystems: nitrate is the dominant form of nitrogen in good to moderately buffered conditions (pH $> 5.0$), while ammonium is inherently very dominant under acidic conditions (pH $< 4.5$). Plant physiology shows that plant species from calcareous or slightly acidic habitats have adapted to nitrate as a source of nitrogen, or a combination of nitrate and ammonium, despite the fact that this is ammonium under acidic conditions (see, for example, Gigon & Rorison 1972; Kinzel 1982).
AMMONIUM TOXICITY

When plant species from growth areas where there was originally virtually no ammonium present as a source of nitrogen, are exposed to increased concentrations of ammonium, a complex of negative phenomena are often observed (see, for example Britto & Kronzucker 2002; Stevens et al. 2011). The physiology of these changes can lead to a significant reduction in growth and development in sensitive species (Figure 2.15).

The negative effects of increased ammonium concentrations and/or an increased ammonium-nitrate ratio on growth and development under laboratory conditions in the Netherlands demonstrated for typical vascular plants and mosses from different habitats: low-nutrient grasslands, species-rich heaths, weakly and very weakly buffered fens, blue grasslands and floating fens (Schuurkes et al. 1986; Roelofs et al. 1996; De Graaf et al. 1998; Lucassen et al. 2003; Paulissen et al. 2004 & Van den Berg et al. 2005). Based on some 300 vegetation samples with geochemical measurements, it was recently found that the presence of typical Red List species in the Pleistocene sand landscape in the Netherlands is strongly correlated with a low ammonium-nitrate ratio and/or low ammonium concentrations in the soil (Kleijn et al. 2008; De Graaf et al. 2009). For example, only two of the Red List species were present with high ammonium-nitrate ratios, while all other remaining Red List species were found in cases where there were (very) low ratios. The opposite was true, however, in the case of the species found in heathland (Figure 2.16). Very recently, studies were carried out on mini-ecosystems with species and soils from low-nutrient environments or with the addition of N in floating fens in Ireland and showed that the negative effects of ammonium may also be prominent in the field (Van den Berg et al. 2008; Verhoeven et al. 2011).

Figure 2.15 Picture of the effect of high ammonium concentration on the growth of leopard’s bane (Arnica montana) after three months of growth in a continuous-flow culture at pH 4 (photo: MCC de Graaf). The plant on the left only has only had (100 µmol/l) in nitrate nutrition and the other plants
beside it have also had ammonium (1000 µmol/l). For the other results from this study, see De Graaf et al. (1998).

**Figure 2.16** The relationship between the ammonium–nitrate ratio in the soil and the soil pH for general plant species (blue diamonds) or Red List species (red squares) from Dutch heathlands. The standard error (SE) is shown in addition to the mean value (Kleijn et al. 2008).

### A CRUCIAL ROLE: THE NITRIFICATION RATE OF THE SOIL

Generally speaking, it can be stated that, for many years, reduced nitrogen has been the major component of total nitrogen deposition in the vast majority of the Netherlands, and that this occurs at an increased rate in areas with a lot of intensive livestock production (see section 2.1). However, this does not automatically mean that the vegetation is exposed to the same ratio of reduced and oxidised nitrogen as the ratio present in the on-site deposition. The ratio of reduced versus oxidised nitrogen that enters the plant is only more or less equal to the ratio present in the air and in the deposition in case of the direct uptake of nitrogen compounds from the atmosphere by aboveground plant components, or the whole organism in the case of mosses and lichens, although reduced nitrogen (ammonium and ammonia) is usually absorbed more easily above ground than oxidised nitrogen (nitrate and nitric oxide). It is also relevant to mention that conditions with limited nitrogen can lead to a substantial part of the nitrogen deposition being absorbed by aboveground plant parts.

In many cases, the ammonium that enters into the soil or water is rapidly converted into nitrate by microorganisms, a process that is known as nitrification. These process releases two protons (H⁺) per nitrogen molecule. The nitrification rate is strongly influenced by the abiotic conditions, in which the pH levels and the amount of oxygen are particularly important. Decreasing pH values from 5 to 4 can cause the nitrification to decrease further, despite the fact that a considerable
level of nitrification can occur in forests even down to very low pH values (3.0–3.5) (Roelofs et al. 1984). Under reduced, oxygen-free conditions, such as those found in permanent wet soil, nitrate is no longer formed from ammonium, except in the root zone of plants that lose oxygen through their roots. Under (alternating) wet conditions, however, nitrate can be denitrified and disappear into the atmosphere as N$_2$ (or sometimes N$_2$O). Bicarbonate is formed during this process and the soil gets ‘deacidified’ (see Intermezzo). All this means that nitrate is still the dominant form of nitrogen as regards the uptake of nitrogen by the vegetation in strong or moderately buffered conditions and areas that are not too wet, even in areas with a high proportion of reduced nitrogen in the air supply. Obviously, this does not apply to mosses and lichens that do not absorb their nitrogen from the soil, but rather directly from the atmosphere or rainwater.

All in all, it can be said that the negative effects of reduced nitrogen may or may not play a prominent role in the degradation of natural and semi–natural ecosystems due to increased nitrogen supply (Bobbink & Lamers 2002; Stevens et al. 2011). In highly buffered conditions (pH $\geq$ 7), most of the plant species present are only adapted to nitrate supply, but are hardly exposed to the negative effects of reduced nitrogen due to the high nitrification rate in the soil or water. Obviously this does not apply to mosses and lichens that were (originally) present in these buffered systems and are exposed to the increased reduced nitrogen values. In systems that are already acidic, such as bogs, heaths and some forests (pH $\leq$ 4.2), ammonium has always been the only source of inorganic nitrogen, which causes the characteristic plant species to adapt to the ammonium supply. The consequence of this is that the aforementioned effects of the increased availability of reduced nitrogen in these systems have much lower effects, or no effect at all. The negative effects are particularly important in those situations where there were originally several plant species that were adapted to nitrate as the dominant form of nitrogen, and not to ammonium supply, and where the soil is only moderately to weakly buffered. The most serious consequences of more ammonium in the plant’s nutrition are therefore mainly found in what were previously weakly to moderately buffered conditions (pH 4.5 to 6.7), for example, as was originally the case in low–nutrient grasslands, very weakly buffered fens, formerly species–rich heathlands and forests on loamy soil. In these systems, the soil or water layer can often be significantly sensitive to acidification. Prolonged exposure to acid deposition, can cause the pH to be so low (pH <4.5) that virtually no nitrification occurs and as a result, high levels of ammonium accumulate in both the soil and plant (Bobbink et al. 1998; Stevens et al. 2011). Sensitive plant species are also threatened by the other effects of soil acidification, such as elevated levels of aluminium and reduced amounts of base cations which cause the susceptibility to ammonium to increase even more (see section 2.3). Several mosses and lichens also experience direct damage, particularly those species that are not adapted to a high uptake and assimilation of reduced nitrogen (Sutton et al. 2009).

2.4 Effects on the habitats of fauna

The previous sections dealt with the effects of nitrogen deposition on soil and water and the vegetation dependent on them. This section outlines what the effects are for animal species. Studies analysing the overall effects of nitrogen deposition on ecosystems analysis almost always fail to study the effects on the fauna. If these are mentioned, it is usually in relation to changes in
the herbivory, and, even then it is only the effects on plants rather than those on the herbivores, that are addressed (e.g. Gilliam 2006). In a few cases, scholars have indicated that there is a gap in our knowledge concerning in wildlife research (Adams 2003).

The direct effects of elevated nitrogen deposition on fauna (section 2.4.5) are rarely dealt with and almost only play a role in aquatic environments. After all, aquatic animals have large and/or thin permeable skin surfaces (gills or tegument) that come into direct contact with the environment for oxygen uptake. This greater exposure means that more immediate effects are to be expected. A large majority of the effects of nitrogen deposition are indirect in nature and come about through chemical processes in soil and water, the resulting changes in vegetation or cumulatively by working their way into the food chain in the case of predators. Due to the fact that these effects occur indirectly and that determining the effect on animals is more difficult to determine than that on the soil, water and vegetation, there is very little scientific evidence available for these effects and the underlying mechanisms. Moreover, the effects of nitrogen deposition interfere with other factors such as depletion, acidification (especially sulphur compounds), changes in land use, climate change, the prevention of invasive alien species and elevated levels of CO$_2$ and O$_3$ in the air (see, for example Rabalais 2002, Fenn et al. 2003ab). This interference has both mitigating and enhancing effects.

Nevertheless, the effects of nitrogen deposition on wildlife can be demonstrated or shown to be (very) likely using both field measurements and experimental studies. Unlike the influence of the nitrogen cycle on vegetation (e.g. Krupa 2003, Bobbink et al. 2010) and on aquatic fauna (Camargo & Alonso 2006), an overview of the mechanisms by which nitrogen deposition can affect terrestrial fauna has never been published in a scientific journal. This is why all processes found in literature studies have been summarised in the diagram shown in Figure 2.17. In the current text, the various processes are developed and supported with citations from the literature. The restorative strategies for habitat types (Part II) and living areas that fall outside these habitat types (Part III) refer to this format of processes as regards the effects on species of the Birds and Habitats Directive (‘protected species’) and typical species (as a quality aspect of habitat types).

A large majority of the effects of nitrogen deposition are indirect in nature and come about through changes in vegetation or water and can have a cumulative effect in the food chain on species in the higher trophic levels. Below we present an overview of the various processes behind the effects of nitrogen deposition on fauna given the relationship between these processes and changes in soil and vegetation described in the preceding sections. These mainly involve the indirect effects of increased biomass production of vegetation due to increased nitrogen availability. These processes are shown in a diagram in figure 2.17. The processes are then discussed and supported by citations from the literature published on this subject.
Increased N deposition

- Increase in N available
- Lowering of pH in water and soil
- Availability of materials
- Disturbed nutrient balance in plants
- Decrease in herbs and low grasses and decrease in flower density
- Decrease in quantity of food plants (in time and/or space)
- Decrease in quality of food plants (in time and/or space)
- Reduction in availability of prey animals and host species (size, quality and accessibility)
- Physiological problems (including impaired growth and osmosis, oxygen deficiency)

1) Cooler and damper microclimate (in time and/or space)
2) Decrease in opportunities to reproduce
3) Decrease in quantity of food plants (in time and/or space)
4) Decrease in quality of food plants (in time and/or space)
5) Physiological problems (including impaired growth and osmosis, oxygen deficiency)

Figure 2.17 Simplified diagram of the impact of nitrogen deposition on animals. Almost all effects have an indirect impact through changes in the soil, surface water, vegetation and litter. Direct effects of the acidifying effects of nitrogen deposition almost exclusively occur through physiological problems in aquatic environments (dotted line).
2.4.1 COLDER AND DAMPER MICROCLIMATE (1)

An increased production of plant biomass creates a higher and denser layer of vegetation (living and dead standing vegetation and a layer of litter) which radiation from the sun is less able to penetrate and less air circulation takes place just above the soil. Heat generation just above the soil is thus inhibited and the overall temperature sum in, or directly on, the soil is lower. The lower temperature and lack of air circulation creates a damper microclimate. Very little research has been carried out into the relationship between nitrogen deposition and the effects of a changed microclimate on fauna. However, the effects listed below are very plausible based on fundamental ecological research on animal species.

A lower temperature sum results in the slower development of invertebrates, making the total development time longer. The development time for the immature stage (egg, larva or nymph) can become so long that the entire life cycle cannot be completed within one season, as demonstrated in the case of locusts by Van Wingerden et al. (1991 en 1992). Research carried out by Schirmel et al. (2011) also showed that a warm and dry microclimate plays an important role in the distribution and diversity of locusts in dry grey dunes.

Larger invertebrate species need a higher overall temperature sum to complete their cycle and they deteriorate earlier and more rapidly than small invertebrates. In the grasslands examined, this leads to the disappearance of these larger species, often in favour of smaller species that can complete their life cycle. When the vegetation structure is replaced in winter (through interventions or natural processes), but closes up again through growth in the course of the season, animal species that need heat for their development in the spring are much less affected by this fallowing than species that require heat in the (late) summer, as has been shown for ants on calcareous grasslands (Van Noordwijk et al. 2011). Those species that are characteristic of open vegetation are resistant to drought and high temperatures. Fallowing causes these species to disappear (such as ground beetles from dune grasslands; Nijssen et al. 2011), probably because they are displaced by less adapted, but more competitive species.

Due to a lower temperature, and a dampening of the air flow, dense vegetation also has a damp micro-climate that can lead to yeast infections in hibernating caterpillars and thus high mortality (Bink 1992, Wallis de Vries & Van Swaay 2006). High, moist vegetation can lead to hypothermia in precocial chicks and therefore an even higher need for food. Frequent or prolonged heating by the parents does not lead to a solution, since this leads to a reduction in the necessary feeding time (Schekkerman 2008).

Interventions to remove the higher vegetation and thick layer of litter do not always lead to an improvement for invertebrates. Grazing leads to shorter, but denser vegetation, which does not sufficiently restore the temperature loss on and in the soil (Wouters et al. 2012). Grazing and a higher frequency of mowing, turf cutting or chopping can all lead to an increase in the frequency of disturbance, making this a limiting factor for – usually larger – species with a long development time. The frequency of the disturbance, in conjunction with the population’s restorative capacity or the species’ recolonisation capacity determines the effect on its local presence (Siepel 1996, Lindberg & Bengtsson 2006, Van Noordwijk et al. 2011).

2.4.2 DECREASE IN OPPORTUNITY TO REPRODUCE (2)

As a result of higher vegetation and the overgrowing of open (or mosaic) vegetation, suitable locations for reproducing become physically inaccessible or inappropriate. This concerns both a nesting opportunity for ground-nesting birds, places to store eggs in the soil, spawning grounds
for fish in open water and mating opportunities. No research has been conducted into the specific relationship between nitrogen deposition and decreased reproduction opportunities for fauna. Based on correlational research into the occurrence of species and overgrowth, however, it appears the aforementioned effects are quite plausible for ants and wasps (Peeters et al. 2004), butterflies (Bink 1992), different kinds of locusts (Lensink 1963, Kleukers et al. 1997) and nesting birds (Van Turnhout et al. 2010). In part, this process interferes with the microclimate becoming cooler and damper and in practice it is almost impossible to determine in many cases whether or not a location is physically inaccessible for reproducing or if the site has become climatically unsuitable.

2.4.3 DECREASE IN QUANTITY OF FOOD PLANTS (3)

Plants are a vital food source for many animal species, both in the form of fresh biomass, dead biomass (litter and humus), flowers (nectar and pollen) and seeds. In this study, a distinction is made between food plants that act as host plants (biomass gets eaten) or those that serve as nectar plants (flowers get visited), wherever necessary. Problems with the availability of food plants for animal species can occur in several ways: (a) The food plants disappear totally or decrease in terms of density or size to the extent that the animal population cannot be provided with sufficient food; (b) The food plants are not available within the activity period of the species in question (mismatch in time), (c) the physical distance between the food plants and other essential landscape elements (such as nesting, hibernation and mating areas, etc.) are irreconcilable. This last point regarding the fragmentation of biotopes within a habitat is discussed in Part III (Landscape ecological embedding of restorative strategies).

A change in the composition of vegetation from herbaceous to more grasses due to the increased availability of nitrogen (Bobbink 1991; Stevens et al. 2004; Clark & Tilman 2008) generally leads to a deterioration of the animal species that use the herbaceous or low, narrow-leaved grasses as specific host plants. Virtually no research has been conducted into the specific relationship between nitrogen deposition and the reduction of food plants, but correlative research on the decline of animal species and the food plants on which they depend, makes this process very plausible. Ockinger et al. (2006) identify a correlation between the decrease in butterfly species and nitrogen deposition and suggest a decrease in (the availability of) food plants. The scarce amount of species-specific research is primarily concerned with pearl butterflies, such as Marsh Fritillary (Fowles & Smith 2006) and Niobe Fritillary (Salz & Fartmann 2009) and ‘checkerspot butterflies’ in North America (Weiss 1999).

Flower visiting insects are dependent on flowering plants for their energy (nectar) and nutrients (pollen – used as a protein for reproduction, for example). Change in vegetation composition – from herbaceous to more grasses due to increased nitrogen availability – can cause a decline in flower visiting insects. This applies both to species that are specialised in one or a few plant species for foraging purposes (Biesmeijer et al. 2006; Fründ et al. 2010) as to species that produce several generations per year, or that build up new colonies every year (e.g. bumblebees) and are therefore dependent on several different plant species for much of the season. Bumblebees that have a wider range of flowers available to them, produce larger colonies (Goulson et al. 2002). In addition, several species of bumblebee – related to tongue length and body size – have different uses for their habitat which decreases the competition for food. This results in several species appearing in a landscape with a diverse range of flowers (Sowig 1989; Westphal et al. 2006; Kleijn & Raemakers 2008).
The diversity, density and quality of flowering plants and the availability of nesting areas (see process 2) also affect the interaction between flowering plants and flower visiting insects that pollinate these plants (e.g. Hoover et al. 2012).

2.4.4 DECREASE IN QUALITY OF FOOD PLANTS (4)

Plants are a vital food source for many animal species, both in the form of fresh biomass, dead biomass (litter and humus), flowers (nectar and pollen) and seeds. In addition to problems in terms of the quantity of these plants (see process 3), changes in the quality of food plants for the animal species can also occur. It is divided into the following processes: (a) a shift in the nutrient balance in the food plant, which means animals cannot access a sufficient amount of essential nutrients; (b) a shift in the relationship between nutrients and antifeeding substances, so that the plant is no longer edible for a particular species of animal; (c) shift of the nutrient balance and/or of the relationship between nutrients and antifeeding substances in the time, leading to the food plant no longer being available within the period of activity of the respective animal species (mismatch in time); (d) shifts in the food quality of a plant which only a few species can benefit from, thus shifting competitive conditions.

Little research has been conducted into the changes in the quality of plant food due to nitrogen deposition. The effects of changes in plant quality on both individuals and populations of herbivorous animals can be significant (Awmack & Leather 2002). There is growing evidence that both the eutrophic and acidifying effects of nitrogen deposition affect the uptake of macro and micronutrients by plants, and thus the food quality of these plants for herbivores (Throop & Lerdau 2004, Nijssen et al. 2011). An interference occurs which causes elevated CO2 concentrations in the atmosphere and climate change (Hoover et al. 2012).

The way in which this change enters the ecosystem through herbivores depends both on the species of plant and the species of herbivore (Throop & Lerdau 2004) and the interaction between them (Throop 2005). Furthermore, most studies report a positive influence of nitrogen deposition on plant quality, expressed in terms of the total N-content of the tissue, sometimes broken down into different types of amino acids. Because herbivores are food for predators, these effects also have an impact higher up in the food chain (see process 6). Plants growing under an increased supply of nitrogen store this nitrogen in the tissue Increased nitrogen deposition can thus change the N: P ratio in plant tissue. This also changes the nutritional value of the plant. This occurs more frequently in systems which are or have become P-limited, through the removal of organic biomass by mowing and cutting sods (Güsewell 2004). In a fertilisation experiment, Ohlson et al. (1995) found that the nitrogen concentration in grass leaves, herbs and dwarf shrubs increased in the undergrowth of forests, where the addition of ammonium had a greater effect than that of nitrate. The increase of nitrogen in the plant tissue was mainly caused by an increase of the amino acids glutamine, asparagine and arginine.

Grey-hair grass (Corynephorus canescens) was shown by Nijssen & Siepel 2010 to store additional nitrogen in non-protein components which are likely to have inhibitory effects on feeding. Mottled grasshoppers (Myrmeleotettix maculatus typical species from the grey dunes) which were bred on nitrogen–rich grey–hair grass showed higher mortality and lower growth than those bred with grey–hair grass without any added nitrogen. Field studies have also shown that mottled grasshoppers in areas with high nitrogen deposition have a lower body weight than mottled grasshoppers from areas with low nitrogen deposition. Aeolian deposition of fresh mineral–rich driftsand actually leads to an improvement in the food quality of grey–hair grass and
consequently to a higher survival and growth of mottled grasshoppers. Furthermore, that aeolian deposition of sand is inhibited by nitrogen deposition, due to the increased production of algae and higher plants.

Depending on the plant species, an increase in absorbed nitrate and/or ammonium can also lead to a higher concentration of proteins and amino acids in plants, so that these plants become more attractive as a food source for insects. This is particularly true for plants that do not possess the ability to create secondary plant substances containing N as a defence. This reaction leads to the formation of an infestation on herbivores and also to shifts in vegetation composition, resulting in a deterioration in the quality of the habitat (see, for example Berdowski 1987).

2.4.5 PHYSIOLOGICAL PROBLEMS (5)

The direct toxic effects of nitrogen compounds (NH4+, NH3, NO2–, HNO2, NO3–) on animals are known only in aquatic environments (e.g. Thurston et al. 1981, Berendzen et al. 2001), where NH3 is the most toxic, and NO3– the least toxic (Camargo & Alonso 2006). In addition, the direct effects of nitrogen deposition occur as a result of the associated acidification. These effects do interfere, given that the pH affects both the (im)mobility of heavy metals and the toxicity of these metals, and of NO3 for wildlife (Schuurkes et al. 1986, Thurston et al. 1981, Leuven et al. 1992, Gerhardt 1993). Interference also occurs through the indirect effects of nitrogen deposition, such as temporary oxygen shortages due to increased biomass growth in vegetation. The effects of nitrogen deposition only really play a role in naturally (moderate) nutrient-poor, not to weakly buffered systems, or in systems that have largely lost their natural buffering capacity through the long–term effects of acidification by sulphur compounds.

The effect of various nitrogen compounds in aquatic systems and the effects on the fauna in these systems has been addressed in various publications (including Rabalais 2002, Camargo & Alonso 2006). The direct effects of acidification concern physiological problems, such as a disturbed ion balance and osmosis or problems in the oxygen levels due to the dysfunctioning of oxygen–carrying proteins (Camargo et al. 2005). These physiological problems can directly cause mortality or impaired development in the immature stage.

Several aquatic animal groups decline significantly or disappear entirely due to acidification. Fish and snails do not occur at pH levels below 5.0–5.2. The disappearance of these groups as a result of acidification is described in Leuven et al. (1986), Leuven & Oyen (1987) en Økland (1992). Other groups of invertebrates (such as amphipods and water fleas) cannot withstand strong acidification. The critical pH value varies greatly by animal species and both enhancing and mitigating effects have been demonstrated due to the presence of heavy metals and minerals – often mobilised as a result of acidification – at the level of this critical value (Vangenechten et al. 1989, Økland 1992, Gerhardt 1993). Nitrate and ammonium in higher concentrations are toxic for aquatic fauna (Berendzen et al. 1987), wherein the toxicity of NH3 increases as the pH decreases (Thurston et al. 1981). In the breeding waters of amphibians, strong acidification causes the direct mortality of embryos, but weaker acidification can lead to a lower hatching success of eggs and a higher degree of damage to the eggs by fungi (Leuven et al. 1986b, Freda 1986).

An additional amount of nitrate or ammonium in water can lead to an increased growth in algae, as long as no other substances such as phosphorous play a limiting role (e.g. Loeb et al. 2010). The large amount of algae can lead to lower oxygen levels. This situation is particularly prevalent in smaller stationary (or slowly flowing) waters; in rivers or large stationary waters, currents and
the wind ensure better mixing and oxygen uptake from the air. Aquatic insects with high oxygen requirements may suffer from periodic oxygen deficiencies (Jeppesen et al. 2000), but this also applies to certain species of fish (De Nie 1997).

2.4.6 Reduction in Availability of Prey Animals and Host Species (6)

Predators and parasitic species are dependent on other animal species to serve as prey or as a host to ensure food supply, or completion of their life cycle. When these animal species experience the negative effects of increased nitrogen deposition, problems may also arise for these predators and parasites. These problems can be divided into the following processes: (a) The disappearance or strong decrease of animal species which causes (a population of) predators or parasites to not have sufficient food or hosts; (b) a decrease in the accessibility of prey animals or host species due to higher and/or more dense vegetation; (c) a reduction in the food quality of prey species; (d) an increase in the physical distance between the prey animals or hosts and other essential elements in the landscape (such as nesting, hibernation and mating areas, etc). This fragmentation of biotopes within a habitat is discussed in Part III (Landscape ecological embedding of restorative strategies). Very little research has been conducted into the specific relationship between nitrogen deposition and the decreasing availability of prey or host species. However, correlational research makes the processes described very plausible. When nitrogen deposition precipitates into ammonium form, this results in acidification of the soil and waters (lower pH value), a reduction in the amount of available calcium and a disturbance of the mineral balance. These effects enter indirectly into the food chain. In waters, such strong acidification leads to effects such as a reduction in fish stocks, which has consequences for fish-eating birds and also for birds with a combined diet of fish and insects. Snails, woodlice, millipedes (all with a calcium-dominated exoskeleton) have disappeared in highly acidified soils and insects produce too little calcium in those circumstances, causing the eggshells of songbirds – which are dependent on these prey – to weaken (Graveland et al. 1994). In the case of black terns, it has been demonstrated that acidic waters do not constitute a suitable habitat due to their lack of fish, which can lead to weak bone structure in chickens (Beintema 1997). The calcium deficiency in invertebrate herbivores is partly reinforced by a lower concentration of their host plants because of the reduced presence of ectomycorrhizal species on the roots. Even birds that are (partially) dependent on aquatic insects, may experience the effects of acidified waters. In the case of dippers, it has been demonstrated that they have a declining population trend in acidified waters, which seems to be directly related to a reduced supply of calcium, resulting in thinner eggshells, smaller eggs and young, and thus a lower rate of reproductive success (Tyler & Ormerond 1992; the fact that weaker animals, whose lower competitiveness levels mean they lose out on the most suitable breeding sites, do not breed by these waters could, however not be excluded). It is expected that other insectivorous birds are also affected by this. In the case of sparrowhawks in nutrient-poor forests, it has been shown that a mineral deficiency in oak leaves has led to the absence of a specific protein that can transport and store vitamin B2 in caterpillars. Although such effects were not observed in the caterpillars that eat the leaves and the (relatively short-living) great tits that mainly feed on these caterpillars, the longer-living Sparrowhawk showed a vitamin B2 deficiency. This resulted in a sharp decrease in breast muscle, low levels of vitamin B2 in eggs and associated fatal embryonic abnormalities (Van den Burg 2000). This may also play a role in other long-living bird species. A cumulative effect of the above is a decrease in the food supply for insectivores. This means that (at times sometimes small) effects of nitrogen deposition can be passed onto species from higher
trophic levels. A reduction in the food supply is caused by both a lower abundance, lower diversity and reduced visibility or accessibility to potential prey, and by a shift from large to small invertebrate species. The consequences of a reduced average–sized prey for insectivores (birds and bats) are described by scholars such as Siepel 1990, Beintema et al. 1991 en Schekkerman & Beintema 2007. The combined effect of smaller prey and a less diverse supply of prey (which may cause a temporary lack of food) in relation to nitrogen–related fallowing in dune areas, is described by Kuper et al. (2000).

2.5 Literature


Bobbink, R., Heil, G.W. & Scheffers, M. 1990. Atmosferische depositie van NOx op bermvegetaties langs autosnelwegen. Vakgroep Botanische Oecologie en Evolutiebiologie, Rijksuniversiteit te Utrecht, 64 pp. (Translation: The atmospheric deposition of NOx on roadside vegetation along motorways.)


Nijmegen, 248 p. (Translation: Effect-oriented measures against the acidification and
eutrophication of moderately mineral-rich heathlands and low-nutrient soils.)

Biodiversity, vegetation gradients and key biogeochemical processes in the heathland


Ammoniak in Nederland. Rapport Planbureau voor de leefomgeving, 500125003,
Bilthoven. (Translation: Ammonia in the Netherlands.)

De Nie, H.W. 1997. Atlas van de Nederlandse zoetwatervissen. Media publishing,
Doetinchem, 151 pp. (Translation: Atlas of Dutch freshwater fish.)

importance of incorporating forest edge deposition for evaluating exceedance of

gevolgen van ingezet beleid. Wageningen, Alterra Wageningen UR, Rapport 1699,
88pp. (Translation: Acidification: causes, effects, critical loads and monitoring of the effects of the
established policy.)

De Vries, W., A. Breeuwsma & F. de Vries 1989. Kwetsbaarheid van de Nederlandse bodem
voor verzuring. Een voorlopige indicatie in het kader van de Richtlijn "Ammoniak en
Veehouderij". Wageningen, DLO-Staring Centrum, Rapport 29, 74 pp. (Translation: Vulnerability of Dutch soil to acidity. A preliminary indication under the ‘Ammonia and Livestock’
Directive.)

intensively monitored forest ecosystems in Europe and their relationships with stand and site characteristics. Environmental Pollution 148: 501–513.


inorganic nitrogen leaching in European forests using two independent databases.


biodiversity. In: The European Nitrogen Assessment, ed. M. A. Sutton, C. M. Howard, J.
W. Erisman et al.Cambridge University Press.

Dorland, E. & A. van Loon 2011. Verkenning kwantificering processen ten behoeve van
herstelstrategieën PAS. KWR 2011.008. KWR, Nieuwegein. (Translation: Exploration of
quantification processes for programmed nitrogen approach restorative strategies.)

Draaijers, G. 1993. The variability of atmospheric deposition to forests. The effects of

Cambridge.


Part I – November 2012 version –


