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## Ammonia exchange between crops and air

Agricultural University of Norway – Advisory Service, Ås Norway

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# Ammonia exchange between crops and air

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The chemical, biochemical and physiological factors that govern the exchange of $NH_3$ between plants and air are reviewed together with methods for measuring the gas exchange. The $NH_4^+$ concentration and pH in plant cells differ between organelles. $NH_4^+$ concentrations in the range of 1-50 mM and apoplast pH in the range of 5.3 – 7.0 have been reported. Physiochemical calculations indicate that such $NH_4^+$ concentrations enable crops to emit $NH_3$ under most circumstances during daytime when stomata are open. The amounts emitted depend on interacting environmental and physiological factors. High temperatures enhance emission of $NH_3$. The studies reviewed indicate that crops are net emitters of $NH_3$ to the atmosphere. Whilst losses are highly variable between crops and seasons it is suggested that for arable crops in temperate regions net losses of $NH_3$ to atmosphere are of the order of 1-2 kg $NH_3N$ $ha^{-1}$ $y^{-1}$.

Key words: Ammonia, ammonium, atmosphere, crops, gas exchange, nitrogen metabolism, pH, temperature.

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## 1. BACKGROUND AND AIM OF THE REVIEW

Agriculture raises environmental issues (Bøckman et al. 1990). An important set of such issues concern losses of nitrogen compounds. Present knowledge about the numerous and interacting factors that determine the extent and impacts of these losses is impressive, as is evident from recent reviews about

- nitrate leaching to ground and surface waters and associated health issues (Addiscott et al. 1991, Walker 1990)
- soil emission of nitrous oxide and nitrogen oxide (Williams et al. 1992, Granli & Bøckman 1994)
- loss of ammonia to the atmosphere (Asman 1992, ECETOC 1994).

Losses of ammonia to the atmosphere are an environmental issue because

- increased deposition of ammonia increases the N input to forests and heathlands, which in turn can change the composition of the vegetation, increase the rates of soil acidification and nitrous oxide emission, and alter the balance of nutrient in the ecosystem
- the loss of ammonia from agriculture represent a waste of resources

- high ammonia concentrations from animal stables and manure spreading can be a local nuisance.

It is well known that ammonia emissions to the atmosphere comes mainly from farm animals and spreading of their manure, some also from application of mineral fertilizers, notably from surface application of urea.

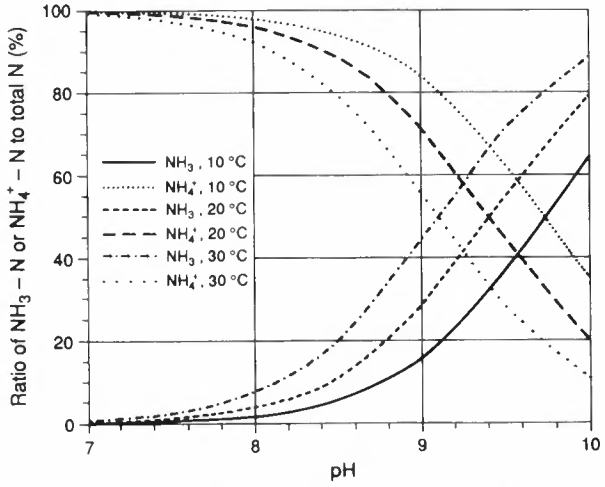
It is also well known that crops take up and give off ammonia through their leaves, but the evidence indicates that crops are a minor source of ammonia to the atmosphere compared with present emissions from livestock. Plants can act both as a source and sink of $NH_3$ (Farquhar et al. 1983, Sutton 1990, Schjørring 1991).

The aim of this study is to
- describe the principal physiological mechanisms that are involved in ammonium assimilation and formation in plants as a background to the main discussion
- discuss biochemical and physiological factors influencing the ammonia exchange
- survey experimental methods commonly used in the study and quantification of ammonia-uptake and -loss from plant parts above ground
- review the magnitude of N-losses observed.

The literature is covered up to the end of 1992. Later papers are less completely covered due to the time delay between publication date and reports in abstracting journals.

## 2. ASSIMILATION AND FORMATION OF AMMONIA IN PLANTS

A background knowledge of the biochemistry of ammonia in plants is useful for insight into the dynamics of ammonia uptake and losses. Hence we will describe briefly the chemical and physiological processes that are involved in ammonia assimilation and formation.




*Figur 1. Effect of pH on relative amounts of ammonium-N and ammonia-N in solution at three different temperatures (ECETOC 1994).*

In aqueous solution, e.g. in the wet surfaces in the substomatal cavities, ammonia exists in instantaneous equilibrium with ammonium;

(1) $NH_4^+$ <-----> $NH_3 + H^+$

The equilibrium is influenced by temperature and pH which in turn depends on metabolic processes. The effect of pH on the relative concentration of ammonium and ammonia in solution at three different temperatures is shown in figure 1. Below pH 7.0 less than 1 % of total ($NH_3$ + $NH_4^+$) species will be available as $NH_3$. We will therefore use the form ammonium as a collective term for both forms, and ammonia when this form is specifically intended.

There also exist an equilibrium between ammonia in aqueous and gas phase in the solution and between gas phase in solution and air;

(2) $NH_3(aq)$ <-----> $NH_3(g)_{solution}$ <-----> $NH_3(g)_{air}$

The exchange of ammonia between solution and air is further discussed in section 2.3.

When we refer to published results with non-SI units, we will as far as possible convert the figures to SI units in brackets.

## 2.1 Assimilation from soil

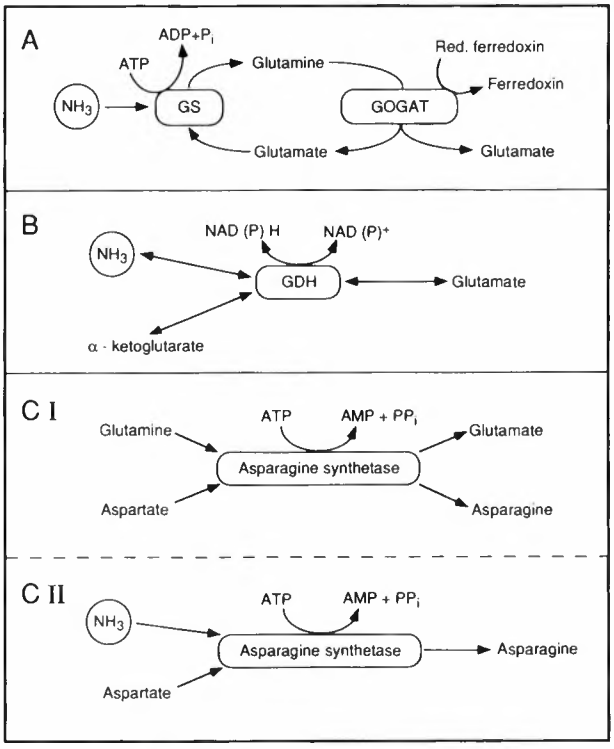
Some plants (e.g. conifers) take nitrogen from the soil mainly in the form of ammonium. Many crops (e.g. cereals) take some of their nitrogen supply in this form, and legumes obtain some ammonium from symbiosis with nitrogen fixing bacteria. However, nitrate is the major source of N to crops. Nitrate taken up from the soil is either converted to ammonium in the roots by the action of *nitrate* and *nitrite reductase* or is transported to the shoot before assimilation.

The most important pathway of ammonium assimilation involves two reactions operating in a cycle. These reactions are catalyzed by the enzymes *glutamine synthetase (GS)* and *glutamate synthase (GOGAT)* (fig.2A). The amino group in glutamate can be transferred to other keto acids in transamination reactions, which are catalyzed by *aminotransferases.* The final products of these reactions are the various amino acids found in plants.

The GS/GOGAT cycle is now believed to be the usual pathway of ammonium assimilation at normal intracellular concentrations. Ammonia assimilation is not a once and for all process because ammonium is released and reassimilated in large amounts at different stages of the plant's metabolism. It seems certain that the GS/GOGAT cycle is operating also in the reassimilation process.

The root system must be able to overcome a potential ammonium toxicity when ammonium is the dominant form of nitrogen in soil, as it is in acid soils or for a short period after application of ammonium-based fertilizers or urea. In this case other potential routes of ammonium assimilation might come into operation:

*Glutamic dehydrogenase (GDH),* catalyses the reaction between α-ketoglutarate, ammonium and NAD(P)H to form L-glutamate and oxidized coenzyme and it also readily catalyses the reverse reaction (fig.2B). However, controversy still exists as to the role of GDH in higher plants. This enzyme has a low affinity for ammonium




*Figur 2. Assimilation of ammonia in plants by*
*A) glutamine synthetase/glutamate synthase (GS/GOGAT)*
*B) glutamic dehydrogenase (GDH) and*
*C) asparagine synthetase.*

since $K_m(NH_4^+)$ ranges from 5 to 70 mM (Stewart et al. 1980) and is only present in relatively small amounts. Experiments by Robinson et al. 1991 with carrot cells provide evidence that the primary role of GDH is the oxidation of glutamate and that GDH is not involved in ammonium assimilation.

The *asparagine synthetase* normally transfers the amide nitrogen from glutamine to aspartate, thereby producing asparagine (fig.2C.I). When excess ammonium is available, asparagine synthetase mediates the reaction between ammonium and glutamate or aspartate and the amides glutamine and asparagine are synthesized (fig.2C.II).

Accumulation of asparagine and glutamine takes place when plants are supplied with high levels of inorganic N, and in particular with ammonium-N.
Further details of mechanisms and of compartmentation of nitrogen assimilation in higher plants was recently reviewed by Lea et al. (1992) and Sechley et al. (1992).

## 2.2 Assimilation from air

Most gas exchange by terrestrial plants is assumed to occur by diffusion through stomata (e.g. van Hove 1987). The molar flux density, J (mol $m^{-2}$ $s^{-1}$), of ammonia entering the leaf is then determined by (Cowan 1977):

(1) $J = 1000g\ (n_a - n_i) / P = 0.1414g\ (n'_a - n'_i) / P$

where:

| | |
|---|---|
| g | – conductance to diffusion of ammonia through stomata and the boundary layer surrounding the leaf (mol $m^{-2}$ $s^{-1}$) |
| $n_a$ and $n_i$ | – partial pressure of ammonia in ambient air and intercellularly (Pa) |
| $n'_a$ and $n'_i$ | – concentration of ammonia in ambient air and intercellularly (µg $m^{-3}$) at 293 K |
| P | – atmospheric pressure (Pa). |

Stomata of most plants open at sunrise and close in darkness, and the light intensity dominates the magnitude of the total diffusion resistance (Aneja et al. 1986). It is the concentration of $CO_2$ in the leaves that controls the stomatal aperture, and removal of $CO_2$ by mesophyll cells during photosynthesis is the main reason that stomata of most species open in light. The water potential within a leaf also has a powerful effect on stomatal opening and closing. As water potential decreases (water stress increases), the stomates close. This effect can override low $CO_2$ levels and bright light. High temperatures (30 to 35 °C) usually causes stomatal closing. This might be an indirect response to water stress, or a rise in respiration rate might cause an increase in $CO_2$-concentration within the leaf. Sometimes stomata partially close when the leaf is exposed to gentle breezes, probably because more $CO_2$ is brought close to the stomata, increasing its diffusion into the leaf. Wind can also increase transpiration, leading to water stress and stomatal closing.

However, calculations by Denmead et al. (1976, 1978) indicate that ammonium absorption by plant foliage appeared to be too large in magnitude to be accounted for by stomatal uptake alone. Plant surfaces are usually moist during nighttime and early morning due to guttation and dew formation. Harper et al. (1987) found that a wheat *(Triticum aestivum)* canopy took up ammonia even during night, and suggested adsorption into the surface moisture as the first step in the uptake. Their calculations of the partial pressure of ammonia in dew indicated a large partial pressure gradient from the air to the dew. The ammonium may then be taken up by ionic diffusion through the leaf surface, apparently through the cuticle. That ammonium can be taken up through leaves is shown by the well established procedure using of ammonium nitrate as a fertilizer for leaf application (Bowman & Paul 1992).

Once passed through cuticula or the stomatal pore and cavity, ammonium is likely to dissolve in the waterfilm of the mesophyll cells in the substomatal cavity before it passes through the cell wall and plasmalemma. This process is discussed in section 4.1. Emission of ammonia proceeds in the opposite direction: Both processes may occur, depending on circumstances.

A more detailed discussion of stomatal behavior and environment is presented by Cowan (1977) and Zeiger (1983).

## 2.3 Concentration in air and the compensation point for ammonia

Concentrations of $NH_3$-N in air in rural areas is generally within the range from 1 to about 14 µg $m^{-3}$, with about 1 – 6 µg $m^{-3}$ as typical (WHO 1986, Sutton et al. 1993). Andersen (1990) reported that annual ammonia concentration in rural areas in Denmark was as low as 0.3 – 0.8 µg $NH_3$-N $m^{-3}$. For our calculations we assume that

2 μg $NH_3$-N $m^{-3}$ is a representative atmospheric concentration as has been found in Britain (Allen et al. 1988). The concentrations tend to be higher in summertime than during winter.

In areas of intensive animal husbandry ammonia concentrations can be greatly increased, and values as high as 50 μg $m^{-3}$ have been found (Asman et al. 1989). Over oceans and at high remote mountains the concentrations are low, mostly below 1 μg $m^{-3}$. There are reports that the concentrations in urban areas tend to be higher than that in rural areas (WHO 1986), others find no difference (Kruse et al. 1989).

Farquhar et al. (1980) established that plants do have a *compensation point for ammonia*. At air concentrations below the compensation point plants will emit ammonia, at concentrations above, nitrogen will be taken up through the stomata.

The compensation point for several young (20-40 days) plant species was found to be about 2 – 5 μg $m^{-3}$ ammonia-N; near the normal concentration of ammonia in air in agricultural areas (Farquhar et al. 1980). The compensation point increased with increasing temperature; from 2 μg ammonia-N $m^{-3}$ at 26 °C to 5 μg ammonia-N $m^{-3}$ at 33 °C. Harper et al. (1989) also reported a compensation point of about 1.6 μg ammonia-N $m^{-3}$ for their soybean fields. Dabney & Bouldin (1990) reported similar values for an alfalfa *(Medicago sativa)* field. Parton et al. (1988) found a higher value for wheat *(Triticum aestivum)*. Their ammonia compensation point exceeded an average ambient level of 15 μg ammonia-N $m^{-3}$, and their measurements suggested that the compensation point had increased to as much as 40 μg ammonia-N $m^{-3}$ during senescence. Morgan & Parton (1989) reported that the compensation point for wheat increases as plants approaches maturity, from about 13 μg ammonia-N $m^{-3}$ at early grain filling to 23 μg ammonia-N $m^{-3}$ at late grain filling.

The general conclusion from this very limited set of data is that the compensation point is normally around or somewhat above typical ammonia concentrations in clean air and may increase during senescence.

The topic of ammonia compensation point for plants is complicated by the possibility of reactions between atmospheric ammonia and acidic aerosols. Such reactions can keep atmospheric ammonia levels low, thus enhancing ammonia losses from crops (Dabney & Bouldin 1990).

The subject of ammonia and ammonium in air has been reviewed by Warneck (1988), Grünhage et al. (1990) and Sutton et al. (1993), and a more detailed discussion of the compensation point in plants is presented by Denmead (1990).

## 2.4 Ammonium concentration in plant tissue

The partial pressure of ammonia in the substomatal cavities varies with the concentration of ammonium in the leaf apoplast (the «dead» part of the plant; the extracellular material, the cell walls and all the tracheids and vessels in the xylem tissue). The concentration reflects the balance between ammonium-generating and -utilizing processes in the plant. Ammonium-utilizing processes are primarily synthesis of amino acids, nucleic acids and chlorophyll. The most important ammonium-producing processes are nitrate reduction, ammonium uptake through roots, photorespiration, general deamination and protein degradation induced during senescence.

The concentration of ammonium in the plant is supposed to be low because of

the toxic effects of ammonia (see section 2.5). For the same reason N in the vascular tissue is thought to be transported as $NO_3^-$ or organic compounds and only in insignificant amounts as ammonium.

A concentration of 2 mM $NH_4^+$ is said to result in a total uncoupling of photophosphorylation (Halliwell 1984). However, the rate of oxygen uptake in isolated mitochondria in the presence of malate is unaffected by up to 45 mM ammonium; and the oxidation of citrate, succinate, or glycine is not affected by ammonium up to a concentration of 20 mM (Yamaya & Matsumoto 1985).

Also, nuclear magnetic resonance spectroscopy studies now in progress indicate an *in vivo* concentration of ammonium in 3-4 weeks old intact spruce *(Picea abies)* seedlings of up to about 57 mM (A.B. Eriksen & H. Aarnes 1993, pers. comm.).

This is in accordance with the rather high ammonium concentrations that have been reported from crushed tissue and in xylem sap. Schjørring et al. (1993b) found a concentration of soluble ammonium-N up to 7 mmol (kg fresh weight)$^{-1}$ in leaves from barley *(Hordeum vulgare)* plants that had received 120 kg N ha$^{-1}$. With an estimated dry matter content of 15 % of fresh weight, that corresponds to 8.2 mM ammonium. Ranges of free ammonium concentrations observed in wheat *(Triticum aestivum)* was 1-6 and 6-18 mM in leaves and ear components respectively (Maheswari 1992). The amount of ammonium in the needles of spruce *(Picea abies)* was found to be 100 – 500 µg ammonium g dry weight$^{-1}$ (Düball & Wild 1988). This corresponds to a molar tissue concentration of about 4 – 21 m*M*. Guttation droplets (xylem sap) on 3-cm high seedlings of rye *(Secale cereale)*, wheat *(Triticum aestivum)* and barley *(Hordeum vulgare)* contained 5.0 – 8.9 mg/l ammonium or 0.28 – 0.38 mM (Goatley & Lewis 1966). Xylem sap collected as stump exudate from maize *(Zea mays)* contained 6.8 mg l$^{-1}$ ammonium-N (= 4.9 mM) (Ivanko & Ingversen 1971).

There are also reports of very low ammonia concentrations. Stump exudates from 20-days old barley *(Hordeum vulgare)* seedlings grown on nitrate, 1:1 nitrate + ammonium or ammonium at nitrogen concentrations of 2 and 8 mM contained only 0.65 – 1.26 nM ammonium (Lewis et al. 1982). Application of 15 mM $NH_4Cl$ to mustard (*Sinapis alba* L.) seedlings brought about a considerably increase in GS activity and no accumulation of endogenous ammonium (Vollbrecht et al. 1989). In contrast, seedlings of Scots pine *(Pinus sylvestris)* accumulated ammonium in cotyledons and roots and showed no stimulation of GS activity after the same application of ammonium (Vollbrecht et al. 1989).

The reported results vary within a broad range, but there is a sufficient number of measurements to indicate that the ammonium concentration in plants can be about 20 mM and perhaps as high as about 50 mM without markedly detrimental effects.

## 2.5 Toxicity of ammonium/ammonia

It is the unprotonated form, ammonia ($NH_3$), that is toxic to the plant. Biological membranes are generally impermeable to ions unless pores or specific carriers are present. However, small uncharged molecules like ammonia can readily pass through membranes.

Pickard & Minchin (1992) studied the transient inhibitions of translocation in the phloem by the application of ammonium chloride solution (10 mM) to a peeled

region of bean plant *(Phaseolus vulgaris)* stems. At pH 6.5 ammonium was without effect. At pH 11.0 even a brief application inhibited translocation. Hence, they concluded that phloem transport within bean stems is inhibited by dissolved ammonia gas but not ammonium ions.

Ammonia can equilibrate across membranes in the chloroplast and then eliminate the proton gradient established during photosynthetic electron transport and uncouple photosynthetic phosphorylation (Crofts 1967 and Good 1977). Puritch & Barker (1967) found that as ammonia toxicity symtoms progressed in tomato plants *(Lycopersicon esculentum)*, there were gross changes in chloroplast morphology, plastid degradation and loss of chlorophyll. Vines & Wedding (1960) reported that ammonia caused damage to membranes as measured by anthocyanin leakage from beet (*Beta vulgaris* L.) discs. It is, however, unclear what tissue concentration is necessary for such toxic effects.

From fig. 1 it should be obvious that the toxicity of ammonium ($NH_4^+ + NH_3$) does not only depend on the tissue concentration of ammonium or the location in the plant or cell, but also on the pH at that location and on the temperature. It is not possible to calculate to what extent ammonia (the toxic form) is present when the ammonium measurement is not made at organelle or even organ level, and no corresponding pH is measured. The explanation of the high measured concentration of ammonium in plants with no visible damage, might be that the ammonium is located at places with low pH and/or high tolerance for ammonium (e.g. mitochondria).

Further discussion of the influence of pH on ammonia emission is presented in section 4.1.

## 3. AMMONIA EXCHANGE WITHIN THE SOIL-CROP-ATMOSPHERE-SYSTEM

Both soil and plants can emit and take up ammonia depending on circumstances. Ammonia losses from agriculture have been discussed by Buijsman et al. (1987), Denmead (1990), Asman (1992) and ECETOC (1994).

It is known that seedlings exposed to ammonia concentrations above the ambient absorb ammonia gas (Hutchinson et al. 1972, Porter et al. 1972, Hutchinson 1973, Meyer 1973, Cowling & Lockyer 1981, Lockyer & Whitehead 1986, van Hove et al. 1987, Whitehead & Lockyer 1987). The absorbtion rate is found mostly to be linearly proportional with the concentration of ammonia outside the plant. When root-medium N is very low, and atmospheric ammonia is high, all the plant N can be derived from shoot aquisition of ammonia (Faller 1972).

Harper et al. (1989) measured ammonia concentrations at the soil surface and at different sites within and above a soybean (*Glycine max*) canopy. Ammonia was both taken up by and emitted from the canopy. However, the amounts of ammonia taken up from the air were rather small, 3.1±0.7 and 0.4±0.7 kg N $ha^{-1}$ in two experiments.

Lemon & Van Houtte (1980) found evolution of ammonia from the top leaves and from the base of the canopy (quackgrass (*Agropyron repens* L.), soybeans (*Glycine max*) and alfalfa (*Medicago sativa* L.)), and absorption of ammonia by the leaves in midcanopy. The flux density from the soybeans was 0.30 mg ammonia $m^{-2} h^{-1}$ (=2.5 g N $ha^{-1} h^{-1}$) out of the top of the canopy and 0.36 mg ammonia $m^{-2} h^{-1}$ (=3.0 g N $ha^{-1} h^{-1}$) from the top leaves of the alfalfa.

Measurements within the canopy of an ungrazed pasture (*Lolium rigidum* and *Trifolium subterraneum*) at maturity, indicated a production of up to 56 g N $ha^{-1}$ $h^{-1}$ ammonia near the ground surface and almost completely absorption of the ammonia by the plant cover (Denmead et al. 1976). Ammonia emitted by the plants may also be adsorbed by the soil.

Hutchinson et al. (1972) studied one seedling of soybean (*Glycine max*), sunflower (*Helianthus annuus*), corn (*Zea mays*) or cotton (*Gossypium hirsutum*) in a closed chamber with rather high concentrations of ammonia, ranging from 24 to 44 μg $m^{-3}$, and found that the annual ammonia absorption by plant canopies could be about 20 kg $ha^{-1}$ under these conditions. They estimated that a field crop growing in air containing ammonia at such extreme concentrations might satisfy as much as 10 % of the total N-requirement by direct absorption of ammonia from the air. As ammonia uptake should be proportional to the atmospheric concentration, the experiment can be taken as an indication that uptake under more usual conditions (about 2 μg $NH_3$-N $m^{-3}$) should be small.

Leaf absorbtion of gaseous ammonia after application of $^{15}N$ labelled pig slurry on sand between rows of winter wheat (*Triticum aestivum*) was measured by Sommer et al. (1993). A 5 cm and a 43 cm high wheat crop absorbed 2.2 % and 3.3 % of the lost ammonium, respectively. The 43 cm high crop reduced the ammonia volatilization to ambient air from 98 % to 90 % of applied ammonium-N.

Denmead et al. (1993) found that about 20 % of the ammonia emitted from surface applied urea to a sugar cane crop was intercepted and captured by the crop leaves. The ammonia concentration within the canopy was considerably higher than above the canopy.

Pot experiments with wheat (*Triticum aestivum*) fertilized with $^{15}N$-$Ca(NO_3)_2$ in one pot and untagged $Ca(NO_3)_2$ in the 48 surrounding pots (diameter of pots = 18 cm), gave a small but significantly increased content of $^{15}N$ in *all* of the «control plants» at harvest (L. Holtan-Hartwig & A.B. Eriksen, unpublished results).

Taken together these reports indicate that some nitrogen circulation can take place within the canopy of a crop. However, though a crop canopy may be referred to as «closed», it will still, from a ventilation point of view, be very open. Exchange of ammonia between a plant and the surrounding atmosphere will thus only to a minor extent be influenced by ammonia emitted from neighbouring plants.

The existence of this ammonia cycle between soil and plants complicates discussions concerning gaseous N-losses from agricultural land. The fact that nitrogen *oxides* is cycling in a similar way (Johansson 1989, Williams et al. 1992) makes this issue even more complex. Quantitative data are limited both with respect to reduced and oxidized forms. More results, representing various crops, differing in nitrogen status and under different climatic conditions, would be welcome.

Decomposing plant material does also lose ammonia (Janzen & McGinn 1991). Whitehead et al. (1988) found that 20–47 % of the N from cut herbage (*Lolium perenne* L.) was lost through volatilization. However, volatilization during drying and induced senescence was less than 1 % of the herbage nitrogen.

It is also known that guttation droplets and leachates from leaves during rainfall contain ammonium. The experimental difficulties in studying this subject are considerable. The few studies made indicate that substantial amounts of ammonium may be excreted and exposed to the air through these processes (Wetselaar & Farquhar 1980). This topic invites further investigation.

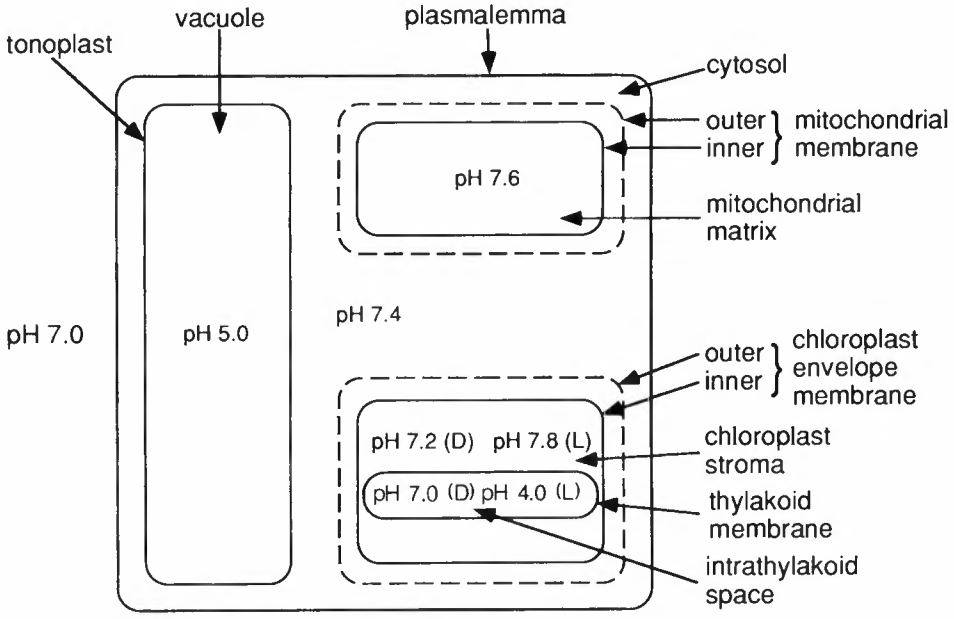
## 4. FACTORS INFLUENCING THE AMMONIA LOSSES

The driving force of ammonia-losses and -gains is the concentration gradient of ammonium between the substomatal cavities and the ambient air. Mechanisms and regulation of ammonia emission are discussed earlier by Farquhar et al. (1983) and considered in detail by Schjørring (1991). We will therefore only briefly discuss the factors influencing ammonia-losses. We will – from a physiochemical point of view - stress the influence of cell compartment pH on the uptake and loss processes.

### 4.1 pH and temperature

Both pH and temperature are of importance when ammonia losses from plants are considered. The influence of pH on the amount of ammonia in equilibrium with ammonium is discussed in section 2. It is clear that an increase in pH strongly increases the potential for ammonia loss. An increase in temperature raises the partial pressure of ammonia in equilibrium with aqueous ammonia in the solution at a given pH, and may then contribute to an ammonia loss.

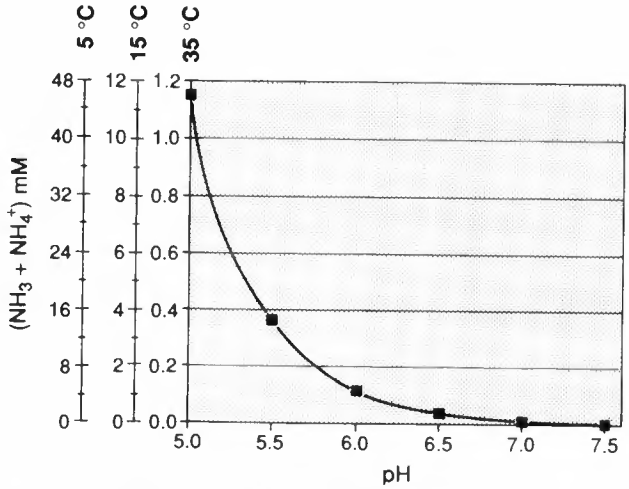
A plant cell in a leaf contains various organelles, each with their own pH. These differ markedly from each other and can also vary with light conditions, nutritional status and physiological age of the plant. Fig. 3 shows the principal compartments in a plant cell and the associated acidity. The xylem sap is found to be slightly acidic, but the phloem sap has a pH around 7-8.5 (Peoples & Gifford 1990).




*Figur 3. The major compartments of a plant cell and their pH values. L=values observed in the light; D=value observed in the dark. From Raven (1985). Redrawn by permission of Blackwell Scientific Publications.*

pH in the photosynthetically active plastides is influenced by light and darkness (see fig. 3). A second environmental factor which changes the intracellular pH is the extracellular pH. Cytoplasmic pH, however, usually changes by less than 0.1 units per unit change in extracellular pH (Smith & Raven 1979, Smith 1984).

The apoplast constitutes the interface between air and the living plant, and it is likely that apoplastic pH (given as 7.0 in fig. 3) is the most important factor for leaf ammonium exchange. pH in the apoplast is, in addition to environmental factors, influenced by internal metabolic and developmental conditions. There are for instance generally lower pH in the cell wall of non-photosynthetic than of photosynthetic cells, and it is well known that the cell wall is acidified during cell expansion. Pfanz & Dietz (1987) found apoplastic pH values ranging between 5.3 in *Taxus baccata* (young needle) and 6.4 in young leaves of *Spinacia oleracea*. pH in the apoplast of sunflower (*Helianthus annuus*) was measured by means of fluorescence to about 5.8 – 6.3 by Hoffmann et al. (1992).




*Figur 4. The equilibrium concentration of total ammonium (ammonia + ammonium) in the apoplast as a function of pH at 5, 15 and 35 °C. The ammonia concentration in ambient air is presupposed to be 2 µg m$^{-3}$. Henry-coefficient by Dasgupta and Dong (1986). Figure from Fjeldberg & Bøckman (1994).*

Fig. 4 illustrates the connection between pH and the equilibrium concentration of total ammonium (ammonia + ammonium) in a solution when the ammonia concentration in ambient air is 2 µg $NH_3$-N m$^{-3}$ and the temperature is 5, 15 and 35 °C. The calculations (Fjeldberg & Bøckman 1994) are based on the formulae given by Dasgupta & Dong (1986). For a fixed value of pH, a value of the total ammoniacal ($NH_3$ + $NH_4^+$) concentration in the solution *above* the curves represent a situation where ammonia can volatilize.

For regions where the atmospheric $NH_3$ concentration differs markedly from 2 µg $NH_3$-N m$^{-3}$ the equilibrium concentration is correspondingly higher or lower. The assumption is made that effects of other solutes can be ignored. The calculation is thus an approximation, but comparison of the equilibrium concentration indicated in figure 4 with the range of reported ammoniacal concentrations in plant cells (about 1-50 mM) and a pH range of 5.3-7.0 and possibly even higher indicate that under most circumstances the plant should be able to emit $NH_3$. The potential for emission should

be less during spring than during summer, as the equilibrium concentration decreases markedly with increasing temperature. High temperature should favour emissions as long as it is not so hot that stomata close. This indicate that $NH_3$ loss through leaves may be more prominent in the tropics and other warm regions than in colder climates.

While these calculations indicate conditions where ammonia emission and uptake is possible, the velocity of the process can not be deduced.

If the wet surfaces in the substomatal cavities are continually losing ammonia, they can be resupplied from the internal parts of the plant cells. Plants can therefore lose ammonia even at relatively low pH values and low concentrations of ammonia and ammonium.

Stutte & co-workers (Stutte et al. 1979, Stutte & da Silva 1981) found a positive correlation between temperature and ammonia losses in their experiments. They suggested that the process of volatile N loss may constitute a defense mechanism of plants against ammonium toxicity under temperature stress.

Possible nighttime uptake of ammonia through plant surfaces wet with dew are not covered by these considerations.

## 4.2 Wind speed and transpiration

In order to lose ammonia the gas must be removed from the crop canopy, it must blow away. With a steep ammonia gradient from leaves to air, the diffusion will be fast. A stagnant boundary layer will prevent the diffusion, and circumstances that preserve such a layer will slow down the exchange rate. Thus gusty winds may enhance losses, even if they are of short duration (Jayaweera & Mikkelsen 1991). At high winds, delivery of ammonia to the exchanging surface rather than the ammonia removal becomes rate limiting. Kissel et al. (1977) report from chamber experiments that the loss of ammonium from fertilizers increases with increasing air flow up to about 15 changes per minute of the air in the chamber.

Ammonia might be lost together with water in the evapotranspiration process, depending on e.g. wind speed, temperature and stomatal aperture. Weiland and Stutte (1978) found a correlation between transpiration and nitrogen loss, but the N-loss was more sensitive than transpiration to temperature variation (Stutte & Weiland 1978).

## 4.3 N supply

Abundant N supply favours ammonia losses, especially if the supply is in excess of normal recommendations for fertilizer application.

Da Silva & Stutte (1981a) found that the N concentration in nutrient solution (20, 40 and 80 ppm N) did not affect the rate of volatile N loss per unit of leaf area of the most recently matured rice (*Oryza sativa*) leaf. However, older leaves supplied with high rates of N (80 ppm N), lost N at a higher rate than those grown in low-N medium (20 ppm N). The release of ammonia per plant part (leaf or ear) from wheat (*Triticum aestivum*) in a field receiving 120 kg N $ha^{-1}$ was greater than from plants receiving 20 kg N $ha^{-1}$ (Maheswari 1992). Experiments by Schjørring (1991a) showed that ammonia emission from barley (*Hordeum vulgare*) are independent of N-level up to 80 days after germination. During the rest of the growing season there was a burst

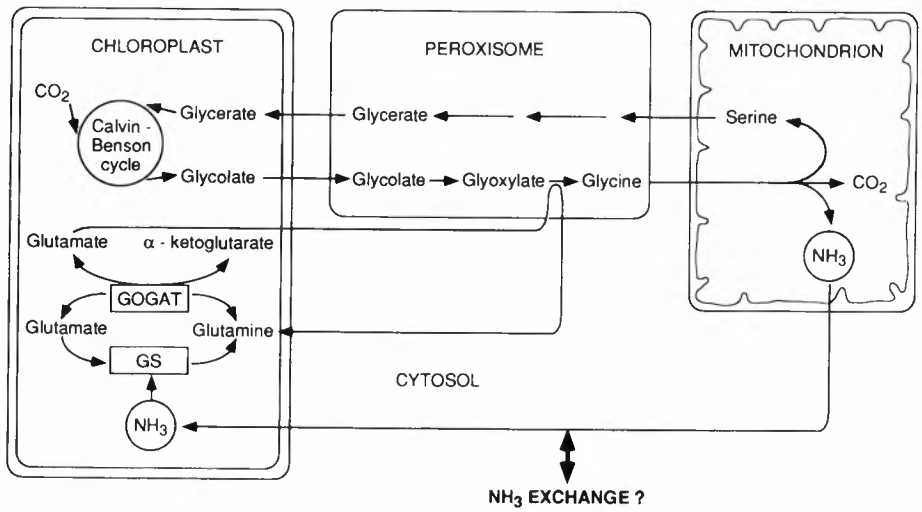
in ammonia emission from the high-N (6 g $NH_4NO_3$-N in pots with 10 kg soil mixture and 35 plants) plants, while the emission from the low-N (0.5 g $NH_4NO_3$-N per pot) plants decreased to nil.

Two distinct periods of emission have been found for winter wheat (*Triticum aestivum*) (O'Deen & Porter 1986, O'Deen 1989), spring wheat (Parton et al. 1988, Morgan & Parton 1989) and spring barley (*Hordeum vulgare*) (Schjørring 1991). The first emission peak is reached at anthesis and the second during final senescence. Schjørring (1991) found that it was the plants supplied with medium and high amounts of N (respectively 2 and 6 g $NH_4$ $NO_3$-N per 10 kg soil per pot with 35 plants) that showed a bimodal volatilization pattern, and that the size of the late peak increased considerably with increasing N supply to the plants. However, Parton et al. (1988) found a bimodal response only in the low-N treatment (no N in nutrient solution added to the pots). The absolute nitrogen loss was higher from the high-N plants (5 mM N in nutrient solution), but the emission curve did not show any peak and losses increased throughout the senescence period. Parton et al. (1988) also found that the N loss rates on a leaf area basis for spring wheat were similar both for plants provided with little and much nitrogen, despite significantly higher N concentrations in the heavily fertilized plants.

Schjørring (1991) pointed out that as the N-supply change, the rate of physiological ageing also change. High N-levels prolongs the development. This should be borne in mind when the differences in ammonia emission are to be interpreted.

## 4.4 Photorespiration

There are indications that photorespiration may form ammonia that can be lost. The reactions involve the chloroplasts, peroxisomes, and mitochondria in the photorespiratory carbon and nitrogen cycle, as shown in fig. 5. Ammonium is formed




*Figur 5. Scheme for photorespiratory C and N cycle. Simplified from Givan et al. (1988). Redrawn by permission of Pergamon Press.*

during the decarboxylation of glycine in the mitochondrium. It is now believed that the majority of the ammonium diffuse out of the mitochondrium and into the chloroplast, where it is reassimilated by GS.

The photorespiratory pathway is open, in the sense that alternate sources of nitrogen and carbon may enter and exit the series of reactions. Ammonia can thus diffuse from organelles involved in photorespiration and into the intercellular spaces (indicated in fig. 5). Then it may be released to the ambient air.

A study of *Sorghum bicolor* (a $C_4$-plant) and soybean (*Glycine max*) (a $C_3$-plant) by Weiland & Stutte (1985) also showed that photorespiration may yield ammonia. Experiments by Morgan & Parton (1989) indicated that the contribution of photorespiratory release of ammonia from wheat to plant total emission could be about 20 %.

Details of the reactions involved in the photorespiratory pathway are discussed by Givan et al.(1988) and Sechley et al. (1992).

### 4.5 Light and darkness

It is generally reported that ammonia emission follows a diurnal trend, with maximum emission at midday and minimum emission or even absorbtion of ammonia at night (Hutchinson et al. 1972, Stutte et al. 1979, Weiland et al. 1982, Ferguson et al. 1988, Schjørring 1991, Schjørring et al. 1993a).

In experiments with spring barley (*Hordeum vulgare*), the ammonia emission reached a stable level only few minutes after the light turned on (Schjørring 1991). When the light was turned off, the ammonia emission immediately declined. Then it was constant for three hours before it declined gradually during the rest of the dark period.

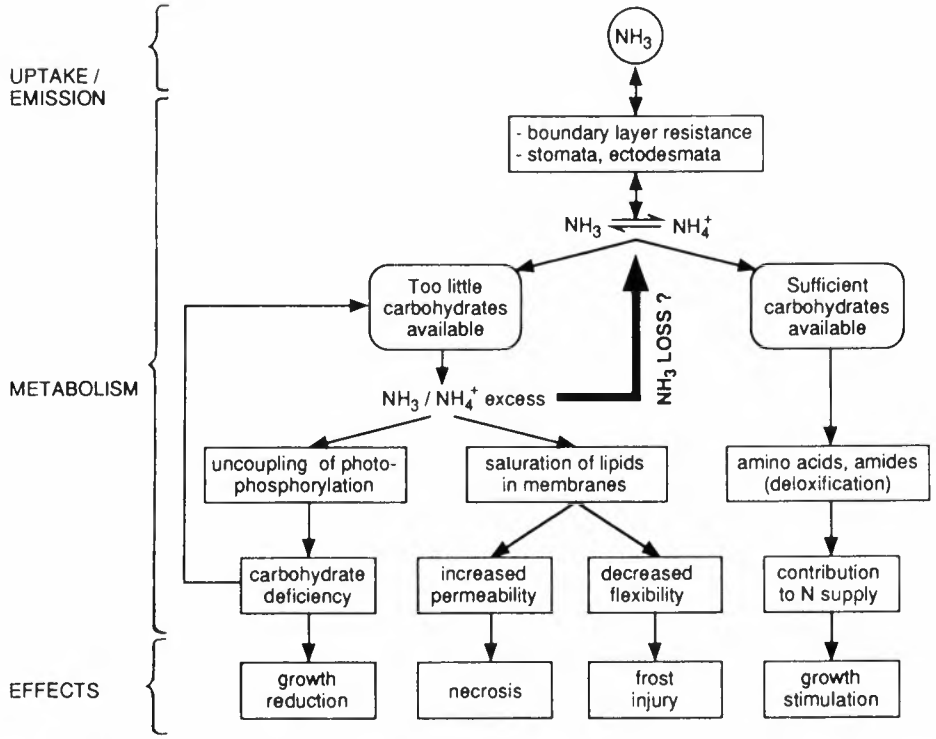
2-6 weeks old snap bean (*Phaseoulus vulgaris*) plants exposed to ammonia levels of 250-593 $\mu g\ m^{-3}$ increased their uptake rates when light was stepped through four levels from 0 to 320 $\mu E\ m^{-2}\ s^{-1}$ (Photosynthetic Active Radiation) (Rogers & Aneja 1980). This increased uptake was closely correlated with the inverse of total diffusion resistance through stomata.

It is probably the effect of light (see section 2.2)) on stomata opening and on photorespiration that increases the potential for ammonia exchange in light.

### 4.6 Availability of carbohydrates

Plants have enzymes able to take care of relatively large amounts of ammonia. As earlier mentioned (section 2.1) the synthesis of amides are important protective processes. The capacity of plants to synthesize amides, and thus detoxify ammonia, depends on the availibility of carbon substrates (Givan 1979).

Remobilization of N in the reproductive phase combined with non-optimal photosynthetic conditions (e.g. drought) may give excess of N relative to C, and result in ammonia losses (fig. 6). From experiments with carrot cells GDH appear to catalyze the oxidation of glutamate (producing α-ketoglutarate and ammonium) in response to a deficiency in carbon. This may enhance the effect of ammonia during




*Figur 6. Metabolism and effects of ammonium in plants with sufficient and insufficient amounts of carbohydrates. Modified from Van der Eerden (1982). Redrawn by permission of Elsevier Science Publishers.*

carbon limiting conditions. It is known that the rate of carbohydrate catabolism increases greatly during periods of active ammonium assimilation (Givan 1979).

Paul et al. (1978) have found that an increased ammonium concentration in the medium caused rapid formation of glutamine, and reactions that feed substrates into the TCA cycle were stimulated at the expense of sucrose synthesis. They suggested that ammonia acts as a regulatory agent in the carbon metabolism of higher plants.

In a field experiment with spring barley (*Hordeum vulgare*) high N losses from the plants and low nitrogen harvest indices (ratio between grain N content and total shoot N content) was found in a year with relatively little photosynthetically active radiation and low air temperatures during grain-filling (Schjørring et al. 1989). Conversely, with more favourable climatic conditions grain yields and nitrogen harvest indices were high and losses of nitrogen low. Thus, nitrogen losses may be related to the capacity of the developing grain to incorporate nitrogen mobilized from senescing plant tissue.

### 4.7 Environmental stress and diseases

Environmentally stressed plants frequently have elevated accumulation of free ammonium in their foliage, which favours ammonia volatilization.

From the work of Feng & Barker (1992a & b) it appears that ammonium accumulation is common in nutrient stressed plants. Tomato plants (*Lycopersicon esculentum*) grown with K, Ca, P or Mg deficiency accumulated more ammonium than plants grown with complete nutrition. Tomato plants grown on ammonium-based nutrition accumulated more ammonium than those grown on nitrate-based nutrition.

Tomato plants subjected to waterlogging had increased ammonium accumulation, as did those subjected to drought (Feng & Barker 1992c). Nilsen & Muller (1981) reported that ammonium concentration in the roots of California shrub (*Lotus scoparius*) was stimulated by water-deficit stress. Also a higher emission of ammonia gas from water stressed plants was found (Weiland et al. 1982).

Application of NaCl or $CaCl_2$ increased ammonium accumulation in tomato plants (*Lycopersicon esculentum*) with nitrate nutrition (Feng & Barker 1992c).

Goulding et al. (1993) reported that severe fungal infection of crops may result in substantial emissions of ammonia.

In experiments using detached barley leaves infected by the powdery mildew fungus *Erysiphe graminis* Sadler & Scott (1974) showed that infection causes accumulation of ammonium. Furthermore, they demonstrated evolution of ammonia gas from these leaves, but Jenkyn & Finney (1984) could not confirm this result. However, in an experiment using *intact* seedlings infection gave greater concentrations of ammonium nitrogen in the senescing leaves and subsequent evolution of ammonia gas from these seedlings (Jenkyn & Finney 1984).

### 4.8 Plant age and senescence

Morgan & Parton (1989) suggested that the increased potential for ammonia volatilization during reproductive growth stages could be attributed to developmental changes in plant N metabolism that elevate tissue concentrations of ammonium above that occuring in younger, vegetative tissue.

When annual plants are maturing there is considerable breakdown of proteins to amino acids. These are exported from the leaves to the developing seeds and accumulated there. Isotopic and total N studies of winter wheat (*Triticum aestivum*) done by Harper et al. (1987) showed that after anthesis about half of the grain N came from remobilization from leaves and stems and the other half directly from the soil. The relative importance for the grain N supply of soil uptake and N derived from senescing leaves vary with environmental conditions, e.g. soil N availability during the grain filling period.

Proteolysis and subsequent deamination of amino compounds can be a source of ammonium during senescence. O'Deen & Porter (1986) suggested that the double-peaked nature of the ammonia emission (see section 4.3) is a consequence of a double burst of acid proteinase activity found in wheat (*Triticum aestivum*) by Dalling et al. (1976).

Maheswari et al. (1992) found that the levels of free ammonium in wheat (*Triticum aestivum*) increased after the leaves expanded fully and especially as the leaves began to senesce. Schjørring et al. (1993b) also found an increasing content of soluble ammonium with leaf age in the flag leaf of barley (*Hordeum vulgare*). Maximum content of ammonium in oldest (lowest) leaves occured slightly before anthesis. Schjørring et al. (1993b) suggest that the decline in ammonium content in

the oldest leaves during the last part of the reproductive growth phase may be due to translocation or ammonia emission, or both.

The proteolysis that occurs in senescing leaves is accompanied by a reduction in the activity of ammonia assimilating enzymes, GS and GOGAT (Foster & Stutte 1986, Schjørring et al. 1993b, Maheswari 1992) and may be an additional cause of the raised tissue concentration of ammonium.

## 5. METHODS FOR MEASURING AMMONIA EXCHANGE

Conclusions on ammonia losses from plants depends on reliable experimental and analytical techniques. A variety of methods are reported for measuring or estimating ammonia emissions from plants. They can be grouped in three categories; enclosure methods, micrometeorological methods and measurements of «standing» N in crops.

### 5.1 Enclosure methods

The enclosure or chamber methods are in common use, they are simple and suitable both for pot experiments and for small field plots. The chambers can enclose one or more plants. An advantage is that they allow separation of growth medium and plant, making it possible to determine the amount of ammonia (or other N-containing gases) that have evolved directly and exclusively from plants. The chambers differ in sizes, shapes, construction materials and consist of two main types; open and closed.

In *open* systems (some are called wind tunnels) ambient air is passing through the chamber. Both the ambient and the outlet concentration is determined. The difference reflects an uptake or loss from the plants.

In *closed* systems there is no contact between ambient air and air inside the chamber during the experiment. A special type of closed enclosure is a plastic bag that is used to enclose one single leaf or a leaflet. Air is passed over the leaf, then through a cold finger in dry ice for condensation, and returned to the leaf. The volume of the condensed leaf vapors are recorded and analysed separately by pyrochemiluminescence for water soluble, nonelemental N form. Reduced and oxidized compounds can be segregated; $10^{-2}$ µg of N can be detected. $N_2O$, NO (and $N_2$) is not detected in the reported process. Researchers applying this technique report N-losses higher than observed by other methods (see appendix). Some of the explanation of the high losses observed might be that $CO_2$ and $NH_3$ is condensed before the air is returned to the leaf. This may lead to enhanced photorespiration, larger stomatal aperture and an enhanced difference in partial pressure of ammonia from inside to outside of the leaf.

In some closed chambers there is no circulation of the air (Recous et al. 1988) while in others a high air exchange rate is established (Wesley et al. 1987). Ammonium volatilization rates measured by enclosure methods are generally sensitive to air circulation speed. Ideally the «windspeed» in the chamber should approximate to that in the field.

In both open and closed systems the ammonia gas (and sometimes other amines) is usually trapped in an acidic solution in gas wash bottles or acid filters. The amount of ammonia is determined with a suitable method, such as colorimetrically,

by steam distillation and titration, potentiometric titration, UV absorption spectrometry or by specific ion electrodes.

It can be difficult to maintain gas concentrations about ambient in the enclosure and to avoid pressure excesses or deficits. In some experiments, the air supplied to the plants in the chamber is scrubbed free from ammonia, amines and $NO\text{-}NO_2$ (Hooker et al. 1980, O'Deen & Porter 1986, O'Deen 1987, 1989, Morgan & Parton 1989). This arrangement might give more ammonia volatilization than under natural conditions.

Another problem is that ammonia may be retained on the walls of the enclosure and air pipes and be dissolved in water condensed in the system.

It is generally difficult in practice to match the enclosure to the outside world with respect to factors that have important influences on the volatilization of ammonia, such as evaporation rate, temperature, wind speed, ambient ammonia concentration and dew formation. Such difficulties are greatest in the closed systems, but might also be of importance in the open systems.

## 5.2 Micrometeorological methods

These methods provide a measure of the average ammonia flux over a large area. Ammonia flux densities measured by micrometeorological methods are the net effect of absorption and desorption by the soil/plant system. They allow continuous measurements and do not disturb the environmental or soil processes influencing gas exchange.

The net vertical transfer is calculated from measurements of wind speed, temperature and the concentration of ammonia at different sites in the field and different distances from the soil surface. Large experimental areas are necessary and very accurate and sometimes very rapid measurements of small gas concentrations. There are various modifications of this principle: gradient diffusion and mass balance methods, described by Denmead (1983) and Lemon & Van Houtte (1980). Eddy correlation techniques cannot be used, as excisting detectors are not sufficiently rapid.

Ferm & Christensen (1987) employed a simplified method using *passive flux samplers*. These require less and cheaper equipment and are less labour demanding than the conventional techniques. The main cost element is the standard automated micrometeorological station. 10-cm tubes with the inside covered with oxalic acid are placed in different positions above the soil surface. The amount of ammonia collected in the tubes is proportional to the product of ammonia concentration and the wind speed along the tube. Schjørring et al. (1992) found good agreement between ammonia emissions measured with the passive flux method and conventional methods in experiments based on the mass balance technique. *The mass balance method* requires establishment of small plots with a markedly different exchange pattern relative to the surroundings, and is not appropriate for measuring ammonia surface exchange fluxes over unaltered ecosystems with low levels of atmospheric ammonia. Such measurements have to be carried out by the gradient method.

In the classic configuration *the gradient method* is based on the use of large homogeneous surfaces. Under such circumstances the air flowing over the surface is assumed to be in equilibrium with the surface up to a given height above the ground. The principles of the micrometeorological gradient approach are based on short sampling periods (1 to 2 hours) in which large changes in conditions are not likely.

The method requires frequent and very precise measurements of the gradients of ammonia concentration, wind speed and temperature over the exchange surface (Denmead 1983), and instrumentation and labour cost are high. This limits the number of places and the time scale over which the method can be operated.

An interesting aspect of the passive flux samplers are that they seem to allow gradient measurements over extended periods (Schjørring et al. 1992). This is not possible with existing methods measuring ammonia concentration and wind speed separately, but it has to be further explored.

With the micrometeorological techniques combined ammonia loss from *plants and soil* can be measured. It is the amount of N escaping from the field which is of environmental interest, but it is not strictly identical with losses from plants.

## 5.3 Measurement of standing N in crops

We use the term *standing N* for the amount of total N (in kg $ha^{-1}$) in plant parts above ground. Changes in this quantity at different developmental stages indicate possible ammonia losses. Some authors also include the N content of roots and even soil, but there are substantial experimental problems with this latter approach. Wetselaar & Farquhar (1980) have reviewed published values of apparent nitrogen losses from tops of plants. Very variable results are reported, ranging from no loss to 80 kg N $ha^{-1}$.

The «standing N» method is an *indirect* measurement, and can not indicate if N is lost as ammonia or in other ways. Wetselaar & Farquhar (1980) gave a list of possible pathways of nitrogen losses from tops of plants: Translocation to roots, root exudates and losses from the soil (by leaching or denitrification) of nitrogen transferred to roots; loss of pollen, flowers, fruits and leaves; loss of plant material by insects, birds, microorganism, as particles breaking off and through excretions leaching from leaf surfaces by rain, dew dripping, sprinkler irrigation or spraying with pesticide; and gaseous losses. These may be as ammonia and other amines, dinitrogen, nitric oxide and nitrogen dioxide, and perhaps even nitrous oxide (Dean & Harper 1986, Guanxiong et al. 1990).

There may also be a considerable loss of gaseous N even if the «standing N» is *increasing*; In a field experiment with winter wheat fertilized with 112 kg $NH_4NO_3$-N $ha^{-1}$ Harper et al. (1987) found that standing N increased through the whole season even during senescence. By micrometeorological methods they observed that nitrogen in an amount equivalent to about 21 % of the applied fertilizer was lost as volatilized ammonia in the same period.

$^{15}N$-enriched or depleted fertilizer is used in more sophisticated measurements of standing N. The measured losses of labelled N from aboveground biomass of corn crops (*Zea Mays* L.) receiving from 50 to 300 kg N $ha^{-1}$ was by Francis et al. (1993) found to be 7 to 34 kg. Assuming no isotope discrimination during volatilization they calculated that apparent real N losses ranged from 45 to 81 kg N $ha^{-1}$.

Schjørring et al. (1989) reported a study where losses of nitrogen from applied fertilizer could be partly separated from that derived from soil mineralization. The content of soil derived (unlabelled) and fertilizer ($^{15}N$-labelled) nitrogen in the aerial parts of the plant was followed during the growing season. They found a $^{15}N$-decline of up to 40 kg N $ha^{-1}$ from field grown spring barley (*Hordeum vulgare*). The total N loss ($^{14}N$ + $^{15}N$) from the aerial plant parts was, however, less than this; 17.8 kg N $ha^{-1}$.

The $^{15}N$ experiments are enigmatic. The results of Schjørring et al. (1989) and of Francis et al. (1993) can be taken as an indication of extensive gasous losses and exchanges of $^{15}N$ taken up by the crops. However, results have also been published from experiments where plants have been given $^{15}N$, and where virtually all $^{15}N$ has been recovered under circumstances where leaching and losses from denitrification have been minimized (Powlson et al. 1992, Recous et al. 1992). It therefore seems that under certain conditions ammonia losses and exchange can be substantial, but that these conditions do not always occur.

Both Schjørring et al. (1989) and Francis et al. (1993) describe experiments where $^{15}N$ content in the plants decreases *relative to* $^{14}N$ during the late growth stages. This might be explained by an uptake of soil derived N ($^{14}N$) in the same period, which will dilute the $^{15}N$ content of the plant. But ammonia exchange between plant and atmosphere may also contribute: A plant containing an excess of $^{15}N$ will then lose $^{15}N$-$NH_3$ (and $^{14}N$-$NH_3$) and gain $^{14}N$-$NH_3$ from the surrounding air. This will result in a decline of $^{15}N$ in the plant relative to $^{14}N$, even if there is no net loss of ammonia. The magnitude of the $^{15}N$ losses observed by Schjørring et al. (1989) and Francis et al. (1993) implies that interpretations of results from experiments with $^{15}N$ uptake by plants carry a substantial degree of uncertainty. This topic requires further clarification.

## 6. MAGNITUDE OF LOSSES

Many researchers have reported loss of ammonia from plants (appendix). Generally there is a net uptake of ammonia during the seedling stage and a net loss immediately after fertilizer application and from anthesis to maturity. This corresponds to the period of commonly observed decline in standing N (Wetselaar & Farquhar 1980). It is also observed that periods of soil N insufficiency can be associated with atmospheric ammonia flux *into* the plants (Sharpe et al. 1988).

It is reported that plants can release nitrogen oxides, but under normal physiological conditions the major part of nitrogen volatilized seems to be in reduced forms e.g. as ammonia or volatile amines (Weiland & Stutte 1979). However, the amounts of N lost as N-oxides have been reported to be as high as 12 to 24 % of the gaseous N loss. Plants being exposed to high air temperature and moisture stress, as well as older plant tissue show a higher percentage of oxidized N-loss than young plants, plants at low air temperature and those receiving appropriate amounts of water ( Weiland et al. 1982). The emissions of nitrogen oxides from plants as distinct from soil is not an easy topic to study, especially under field conditions. However, a resumption of studies on this topic seems desirable in view of the current interest of emissions to the atmosphere of NO and $N_2O$.

*The magnitude* of N-losses observed by use of different methods and for different species and developmental stages are listed in appendix. Where estimates/-measurements of daily or seasonal N-losses per ha are not given, the daily N-losses per ha are estimated from the reported values so that the results can be compared.

The table in the appendix shows a rather broad range of results. Both emissions and gains have been reported, but as a whole arable crops appear as a net source of atmospheric $NH_3$. The emissions mostly fall in the range of 5 – 50 g $NH_3$-N $ha^{-1}$ $d^{-1}$, with the majority of the measured losses below 35 g $NH_3$-N $ha^{-1}$ $d^{-1}$. As emissions vary

with conditions of temperature, water status and plant development stage, daily emissions can not be directly converted to yearly losses. However, where yearly losses are reported they mostly are in the range of 1 – 2 kg N $ha^{-1}$. When conditions are unfavourable for high crop yields, emissions can be larger. The correspondence between the data set between daily and yearly emissions seems reasonable.

Most of the reported measurements are from cereals, but the results listed in appendix indicate that other crops also have similar emissions of $NH_3$.

The high figures of N loss from some standing N measurements do not fit with other observations. For instance, a net emission in the late summer of for instance 15 kg $NH_3$-N $ha^{-1}$ from the 79.6 x $10^6$ ha of arable land in Western Europe (EC + EFTA nations) implies a loss of about 1.2 Mt $NH_3$-N $year^{-1}$ or about 30 % of *total* ammonia emission (ECETOC 1994). A seasonal emission of this magnitude should give a noticeable increase in depositions during the ripening period, which is not observed. It is thus likely that the decline of standing N is not only due to ammonia loss from the plants, or that high values of the decline are not representative.

## 7. CONCLUSIONS

All methods used for measuring ammonia exchange between air and plants/crops have their problems. The micrometeorological methods seems to give the most reliable data of crop emissions of ammonia to the atmosphere, but there are only a few sets of micrometeorological measurements of ammonia exchange from non cereal arable crops.

There are no reports where all different types of methods are intercalibrated, and it is therefore difficult to compare results. Field studies made on the same field with all the different methods througout the growing season would be helpful, particularly if the studies could be made for a few consecutive years and on sites with different climates.

Plants both take up and lose ammonia through their leaves. Generally there is a net loss of ammonia through the growing season.

The results listed in appendix lead us to suggest that a net $NH_3$ losses from arable crops of 1.5 kg $NH_3$-N $ha^{-1}$ $y^{-1}$ can be used as calculation factor for $NH_3$ losses from this source. This is a rough estimate, but estimates of $NH_3$ losses from other agricultural sources are also approximate, with a range of uncertainty of +/- 30 to 40 % (Buijsman 1987, Asman 1992, ECETOC 1994). For comparison, Whitehead & Lockyer (1989) estimated that the average annual ammonia loss from decomposing herbage on fertilized grasslands in the UK was 1.4 kg $NH_3$-N $ha^{-1}$.

The ammonia emission from crops is increased if fertilizer or manure is applied in amounts that substantially exceed recommended levels, but this is actively discouraged and is not a common practice.

It is probable that losses will be greater than 1 – 2 kg $NH_3$-N $ha^{-1}$ $y^{-1}$ if the crop is severely stressed by disease or very adverse weather during the grain filling period. Losses may also be higher if the weather is hotter or more windy than usual. The results listed in appendix indicate that a calculation factor of about 6 kg $NH_3$-N $ha^{-1}$ $y^{-1}$ represents a reasonable estimate of losses occuring under such adverse conditions.

The existence of some ammonia interchange between plants within the crop

canopy has been demonstrated, but more studies are required before this exchange can be reliably quantified.

Ammonium (and nitrate) is excreted by guttation and water percolate after rain or irrigation returns nitrogen to the soil. Dew covers the plants during night and early morning, then it evaporates. This permits superficial uptake of $NH_3$ from the air by the vegetation during nighttime. What has not been taken up by the plant during night and early morning will soon be re-emitted to the atmosphere as the vegetation dries (Sutton et al. 1992a). The role of these processes in ammonium exchange between plants and the atmosphere is largely unexplored, though they may be important for diurnal variations in atmospheric ammonia concentrations.

Reports about changes in the total nitrogen content of above-ground parts of crops vary. Some report substantial apparent N losses, others find no change. It is suggested that such losses may be explained by ammonia losses from leaves, but this issue is still unresolved.

Much work has been done on gaseous N loss from crops, but the topic still represent a considerable scientific challenge.

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## 8. APPENDIX

### *Measured and estimated N-losses found by use of different measuring methods and for different species and growth stages.*

(*) When estimates/measurements of daily or seasonal N-losses per ha are not given, the authors of *this* article have estimated daily N-losses per ha on the basis of the measured values. When leaf area index (LAI) is not presented, we have in our estimates fixed it to 4 for all species and developmental stages. In our estimates, emission and uptake is supposed to take place for 12 hours per day.

| Method | Species | Developmental stage | N-losses | | References |
|---|---|---|---|---|---|
| | | | Measured | Estimated | |
| Enclosure | Winter wheat (*Triticum aestivum*) | Prior to flowering | 0.34-0.89 $10^{-1}$ mg (m leaf area)$^{-2}$ $d^{-1}$ | 13.6-35.6 g $ha^{-1}$ $d^{-1}$ (*) | Hooker et al. 1980 |
| | | After flowering | 1.03-1.32 . $10^{-1}$ mg (m leaf area)$^{-2}$ $d^{-1}$ | 41.2-52.8 g $ha^{-1}$ $d^{-1}$ (*) | |
| » » | Winter wheat (*Triticum aestivum*) | Senescing | Up to 2.97 mg $m^{-2}$ $d^{-1}$ | 1.0-1.6 kg $ha^{-1}$ (90 days) | O'Deen & Porter 1986<br>O'Deen 1987<br>O'Deen 1989 |
| | | | | 11-18 g $ha^{-1}$ $d^{-1}$ (*) | |
| | | | | Max. 29.7 g $ha^{-1}$ $d^{-1}$ (*) | |
| » » | Winter wheat [1] (*Triticum aestivum*) | Tillering - harvest | – | Typically 30-37 g $ha^{-1}$ $d^{-1}$ | Recous et al. 1988 |
| | | | | 3.1-4.1 kg $ha^{-1}$ $y^{-1}$ | |
| » » | Spring wheat (*Triticum aestivum*) | Head emergence – maturity | During pre-senescence: 60-120 ng (m leaf area)$^{-2}$ $s^{-1}$ | Typically 63-130 g $ha^{-1}$ $d^{-1}$ from heading to hard kernel | Parton et al . 1988 |
| | | | During final plant senenscence: 200-300 ng (m leaf area)$^{-2}$ $s^{-1}$ | 2.8-4.4 kg $ha^{-1}$ from heading to hard kernel | |
| » » | Spring wheat [2] (*Triticum aestivum*) | Seedling - harvest | 0-60 ng (m leaf area)$^{-2}$ $s^{-1}$ | 0-104 g $ha^{-1}$ $d^{-1}$ (*) | Morgan & Parton 1989 |
| » » | Wheat (*Triticum aestivum*) | 26 days after anthesis | 30-43 nmol $NH_3$ $leaf^{-1}$ $h^{-1}$ | – | Maheswari et al. 1992 |
| | | | 77-143 nmol $NH_3$ $ear^{-1}$ $h^{-1}$ | | |
| » » | Wheat (*Triticum aestivum*) | From planting and the 14 following weeks | 0.16 % of applied N | – | Craswell & Martin 1975 |
| » » | Soybean (*Glycine max*), sunflower (*Helianthus annuus*), corn (*Zea mays*) and cotton (*Gossypium hirsutum*) | Seedling | 3.5-5.6 µg (dm leaf area)$^{-2}$ $h^{-1}$ *gained* | Uptake of 20 kg $ha^{-1}$ $y^{-1}$ | Hutchinson et al. 1972 |
| » » | Maize (*Zea mays*) [3] | 78-116 days after gemination | 0-0.57 nmole $NH_3$ (m leaf area)$^{-2}$ $s^{-1}$ | 7 g of N $ha^{-1}$ $d^{-1}$ (LAI=1) from the senescing leaves | Farquhar et al. 1979 |
| | | | | 28 g $ha^{-1}$ $d^{-1}$ (LAI=6) (*) | |

| Method | Species | Developmental stage | N-losses | | References |
|---|---|---|---|---|---|
| | | | Measured | Estimated | |
| » » | Maize (*Zea mays*) | Throughout growing season | -0.3-34.8 ng (m leaf area)$^{-2}$ s$^{-1}$ Average: 13.1 ng (m leaf area)$^{-2}$ s$^{-1}$ | Up to 2 kg ha$^{-1}$ y$^{-1}$ Average: 22 g ha$^{-1}$ d$^{-1}$ (*) | Weiland & Omholt 1985 |
| » » | Rice (*Oryza sativa*) | Seedling harvest | – | 1.9 kg ha$^{-1}$ y$^{-1}$ | Neue et al. 1983 |
| » » | Perennial ryegrass (*Lolium perenne*)[4] | – | 48-224 ng (m leaf area)$^{-2}$ s$^{-1}$ *absorbed* | 6-28 g ha$^{-1}$ h$^{-1}$ *absorbed* (LAI=4) = 72-336 g ha$^{-1}$ d$^{-1}$ (*) | Cowling & Lockyer 1981 |
| » » | Perennial ryegrass (*Lolium perenne*) | Senescence induced by shading | Less than 1% of plant N (70 days) | – | Whitehead et al. 1988 |
| | Cut herbage of perennial ryegrass (*Lolium perenne*) | – | 20-47% of N in herbage (70 days) | – | |
| » » | Kentucky bluegrass (*Poa pratensis*) [5] | (turf) | 4.0-23.0 mg m$^{-2}$ hr$^{-1}$ | 0.48-2.76 kg ha$^{-1}$ d$^{-1}$ (*) | Wesley et al. 1987 |
| » » | Rice (*Oryza sativa*), soybean (*Glycine max*), cotton (*Gossypium hirsutum*), corn (*Zea mays*), sorghum (*Sorghum bicolor*), peanuts (*Arachis hypogaea*), cocklebur (*Xanthium pensylvanicum*), palmer amaranth (*Amaranthus palmeri*), ivyleaf and entireleaf morningglory (*Ipomoea hederacea*), johnsonngras (*Sorghum halepense*), jimsonweed (*Datura stramonium*) | Mainly vegetativ stages | Typically 1-12 µg (dm leaf area)$^{-2}$ hr$^{-1}$ | 15-45 kg ha$^{-1}$ y$^{-1}$ | Foster & Stutte 1986 da Silva & Stutte 1981a and 1981b Stutte & da Silva 1981 Stutte & Weiland 1978 Stutte et al. 1979 Weiland & Stutte 1978, 1979, 1980 and 1985 Weiland et al. 1979 and 1982 |
| Micro-meteoro-logical | Winter wheat (*Triticum aestivum*)[6] | Seedling - harvest | -(70)-650 g ha$^{-1}$ d$^{-1}$ | From plants + soil during a 20-days period after fertilization: 8.3 ±1.9 kg ha$^{-1}$<br>From plants between anthesis and harvest: 7.1 ± 1.5 kg ha$^{-1}$<br>Total: 15.5 kg N ha$^{-1}$ y$^{-1}$ from soil + plants | Harper et. al 1987 and Sharpe et al. 1988 |
| » » | Maize (*Zea mays*) | 70-85 days after planting | When dry soil: 6.6 g ha$^{-1}$ h$^{-1}$ *absorbed*<br>When moist soil: 27.6 g ha$^{-1}$ h$^{-1}$ lost | 79 g ha$^{-1}$ d$^{-1}$ *absorbed* (*)<br>331 g ha$^{-1}$ d$^{-1}$ lost (*) | Denmead et al. 1978 |

| Method | Species | Developmental stage | N-losses | | References |
|---|---|---|---|---|---|
| | | | Measured | Estimated | |
| » » | Soybean *(Glycine max)*[7] | Groowth stage V3 - maturity | (-5)-2.5 g $NH_3$ $ha^{-1}$ $h^{-1}$ | *Absorption* of soil released $NH_3$: 63.0 ± 10.9 g $ha^{-1}$ $d^{-1}$ average over the season | Harper et al. 1989<br>Sharpe et al. 1988 |
| » » | Soybean *(Glycine max)* infested with quackgrass *(Agropyron repens)* | – | Daytime: 4,0 mg $NH_3$ $m^{-2}h^{-1}$ *gained* by the canopy | 395 g N $ha^{-1}d^{-1(*)}$ *gained* | Lemon & Van Houtte 1980 |
| | Soybean *(Glycine max)* | | Daytime: 0,3 mg $NH_3$ $m^{-2}h^{-1}$ lost | 30 g N $ha^{-1}d^{-1}$ lost(*) | |
| » » | Alfalfa *(Medicago sativa)*[8] | Seedling – harvest | 2–3 g $ha^{-1}d^{-1}$ | Day: 1.2 kg $ha^{-1}y^{-1}$ loss<br>Night:1.6 kg $ha^{-1}y^{-1}$ *gain*<br>During harvest:<br>2.3 kg $ha^{-1}$ loss | Dabney & Bouldin 1985 |
| » » | Alfalfa *(Medicago sativa)* grazed pasture | 3 weeks in late summer | 0.8–3 mg $m^{-2}h^{-1}$ | 260 g $ha^{-1}d^{-1}$ | Denmead et al. 1974 |
| » » | *Calluna vulgaris* and *Eriophorum vaginatum* dominated sites | – | $NH_3$, was found to *deposit* rapidly to all the sites investigated | – | Sutton et al. 1992b |
| » » | Ungrazed pasture *(Lolium rigidum + Trifolium subterraneum)* | From 70 cm height until maturity | 2 g $ha^{-1}h^{-1}$ | 24 $ha^{-1}d^{-1(*)}$ | Denmead et al. 1976 |
| | Grazed pasture | – | 13 g $ha^{-1}h^{-1}$ | 156 g $ha^{-1}d^{-1(*)}$ | |
| » » | Spring barley *(Hordeum vulgare)* | Seedling – harvest | 2–40 mg $m^{-2}h^{-1}$ | 0.5-1.5 kg $ha^{-1}y^{-1}$ | Schjørring et al. 1993a |
| » » | Spring barley *(Hordeum vulgare)* | Anthesis and the following 2 weeks | 1-2 nmol $NH_3$ (m leaf surface)$^{-2}s^{-1}$ | 24-48 g $ha^{-1}d^{-1(*)}$ | Schjørring et al. 1991 |
| » » | Fertilized agricultural vegetation | – | Warm and dry conditions: Up to 24 ng $m^{-2}s^{-1}$<br>Wet conditions: $NH_3$ is *deposited* | Up to 20.7 g $ha^{-1}d^{-1(*)}$ | Sutton 1990 |
| » » | Different grasses and crops | – | Range: -0.003-0.12µg $NH_3$ $m^{-2}s^{-1}$<br>Mean: 0.031 µg $NH_3$ $m^{-2}s^{-1}$ | Mean: 11.03 g N $ha^{-1}d^{-1(*)}$ | Harrison et al. 1989 |
| Standing N | Winter wheat *(Triticum aestivum)*[9] | From 25 cm height until maturity | 25-80 kg $ha^{-1}$ | – | Daigger et al. 1976 |
| » » | Winter wheat *(Triticum aestivum)* | Seedling – harvest | Up to 60 kg $ha^{-1}$ in 20-30 days around grain filling | – | Greenwood et al. 1987 |
| » » | Winter wheat *(Triticum aestivum)* | Seedling – harvest | Up to 20 kg $ha^{-1}$ after flowering | – | Mary et al. 1988 |
| » » | Wheat *(Triticum aestivum)* | ? | 14.9-76.9 kg N $ha^{-1}$ | – | Papakosta & Gagianas 1991 |

| Method | Species | Developmental stage | N-losses | | References |
|---|---|---|---|---|---|
| | | | Measured | Estimated | |
| » » | Spring barley *(Hordeum vulgare)* | Seedling – harvest | 5-40 kg $ha^{-1}$ of fertilizer derived N ($N^{15}$)<br><br>0-17.8 kg $ha^{-1}$ of total N in aerial plant parts | – | Nielsen & Jensen 1986<br>Schjørring et al. 1989 |
| » » | Spring oilseed rape *(Brassica napus)* | Seedling – harvest | – | 2.5-31.0 kg $ha^{-1}y^{-1}$[*] | Augustinussen 1987 |
| » » | Maize *(Zea mays)* | Postanthesis – harvest | 45-81 kg N $ha^{-1}$ | – | Francis et al. 1993 |

[1] – N-losses from plant *and* soil
[2] – A peak of $NH_3$ evolution was found at anthesis
[3] – 0 from young and 0.57 nmole from senescing leaves
[4] – Air passing the ryegrass contained $NH_3$ at 16 µg $m^{-3}$, similar to the level above a grazed pasture (Denmead et al. 1974)
[5] – Urea applied foliarly
[6] – The plants absorbed about 1 % equivalent of the applied fertilizer in a period of soil N sufficiency
[7] – Development stages defined by Fehr et al. (1971)
[8] – The alfalfa was not allowed to mature and senescence but was just followed as managed on a farm
[9] – The losses occured during the grain filling period after anthesis

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