Nitrogen uptake and allocation by *Calluna vulgaris* (L.) Hull and *Deschampsia flexuosa* (L.) Trin. exposed to $^{15}NH_3$

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SUMMARY

The transition of Dutch heathlands dominated by *Calluna vulgaris* to grass heaths occurs rapidly and is primarily ascribed to nitrogenous air pollution. *C. vulgaris* and *Deschampsia flexuosa* were fumigated with $^{15}NH_3$ and the adsorption of ammonia to the leaf surface as well as the uptake and translocation of ammonia nitrogen was determined after 4 and 9 weeks.

There appeared to be little or no NH_3-nitrogen adsorbed to the leaf surface of either species. *D. flexuosa* took up more NH_3 per unit shoot weight, especially during the first 4 weeks of fumigation. The proportion of nitrogen in the shoots of *C. vulgaris* taken up as NH_3 was approximately 6% and 15% after 4 and 9 weeks exposure to NH_3, respectively, while corresponding proportions for *D. flexuosa* were approximately 17% and 28%. The nitrogen fraction derived from the foliar uptake of NH_3 was a factor 1·5 higher in the roots of *D. flexuosa* than in the woody parts and roots of *C. vulgaris* after 9 weeks fumigation. Regular spraying with tap water did not influence the concentration of nitrogen or that of cations in either species.

The uptake and allocation of NH_3-nitrogen in the two species is discussed in relation to growth and consequences for competition in the field.

Key-words: Calluna vulgaris, Deschampsia flexuosa, foliar uptake, heathlands, $^{15}NH_3$, nitrogen, translocation.

INTRODUCTION

Much of the total heathland area in the Netherlands has developed into grassland vegetation predominated by *Deschampsia flexuosa* (L.) Trin. and *Molinia caerulea* (L.) Moench. The total area of these grasses has rapidly increased at the expense of *Calluna vulgaris* (L.) Hull (Gimingham & De Smidt 1983; Heil & Diemont 1983; Heil & Bruggink 1987; Van Kootwijk 1989). The nutrient-poor, sandy podzols on which the Dutch heaths grow, are sensitive to acidification and eutrophication (Van Breemen *et al.* 1982; Ellenberg

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1987) and changes in species composition on such soils correspond to the accumulation of humus and litter and an increased availability of nitrogen and phosphorus (Roelofs 1986). Air pollution is considered to be the most probable cause for this change (Roelofs *et al.* 1985; Van Dam *et al.* 1986). The deposition of nitrogenous air pollutants, responsible for approximately 60% of the annual acidification in the Netherlands, has increased considerably during the last decade to mean values of 40 kg N ha^{-1} y^{-1} (Anonymous 1989) and extremes of up to 140 kg N ha^{-1} y^{-1}. The increase is largely accounted for by NH$_3$ emissions originating from intensive livestock farming practices, so that currently the wet and dry deposition of NO$_x$ and NH$_y$ each accounts for half of the average total nitrogen deposition.

Thus, in rural areas where NH$_y$ deposition is high, it will inevitably stimulate plant growth in a species specific manner, altering relative competitive abilities under conditions in which nitrogen limits growth. The increased relative growth rates due to nitrogen fertilization by NH$_y$ is thought to be responsible for the shift in relative competitive ability between *C. vulgaris* and the grasses *M. caerulea* and *D. flexuosa*. To date, nitrogen fertilization by NH$_3$ has been considered in terms of total NH$_y$ deposition. There has been little differentiation in the manner of uptake of NH$_y$-nitrogen, uptake by the roots via the soil or through foliar uptake.

Also, the manner in which nitrogen is taken up by plants exposed to high atmospheric concentrations of NH$_3$ has not been quantified. Apart from possible growth stimulation, direct toxic effects may occur if atmospheric NH$_3$ is readily absorbed by foliar uptake to very high concentrations. Furthermore, differences in nitrogen uptake may lead to different patterns of nitrogen allocation per species. In the experiment described here, *C. vulgaris* and its competitor *D. flexuosa* were fumigated with labelled NH$_3$ to study mechanisms with respect to the foliar uptake of atmospheric nitrogen and its translocation from leaves to woody stems and roots. The effects of NH$_3$ fumigation on the growth and mineral concentrations of both species were also examined.

MATERIALS AND METHODS

Plants

Plants were sampled in autumn 1987 from a dry heathland vegetation on the nature reserve 'Asselse Heide' (52°12′N, 05°51′E) near Apeldoorn in The Netherlands. Individual plants of *Calluna vulgaris* (L.) Hull (3–5 years old) and small tussocks of *Deschampsia flexuosa* (L.) Trin. were collected with soil cores, diameters 10 and 5 cm, respectively. They were potted into 1·5 l pots filled with topsoil taken from the same site and placed in a glasshouse.

Treatments

In February 1988, 70 plants from each species were divided into seven homogeneous groups. One of the groups was immediately harvested. The remaining six groups were placed in a glasshouse and exposed to NH$_3$. Four groups received their water supply via the pot and tray, while the other two were regularly sprayed from above with tap water three times weekly. One half of the plants was harvested after 4 weeks and the rest after 9 weeks of exposure to NH$_3$. At harvest, one of the plant groups that had been watered via the pot was thoroughly rinsed (30 s) to wash adsorbed nitrogen resulting from dry deposition, from the leaves.

Fumigation and climatic conditions

The fumigation glasshouse was situated in a larger glasshouse and was ventilated through charcoal-filters to remove pollutants from the ambient air. The glasshouse (area $12 \, m^2$, volume $30 \, m^3$) was vertically ventilated with $90 \, m^3$ air min^{-1}, resulting in an air velocity of *circa* $0 \cdot 11 \, m \, s^{-1}$. The air temperature in the glasshouses was maintained at 20°C during the day and 15°C at night. Relative humidity (40–65%) and light intensity were more variable, depending on the weather conditions outside. Additional illumination was supplied to $25 \, W \, m^{-2}$ at plant height, $12 \, h \, d^{-1}$.

NH$_3$ fumigations were realized by bleeding pure NH$_3$ from a cylinder into the airstream via thermal mass flow controllers (Brooks 5850 TR). Ammonia was measured with a chemiluminescent nitrogen oxides analyser 8840, preceded by a thermo convertor 8750, both from Monitor Labs. The average concentration was $100 \, \mu g \, m^{-3}$ NH$_3$.

Labelled NH$_3$ was also bled into the airstream via a thermal mass flow controller. The amount of labelled nitrogen in the airstream was 0·44595%.

Plant analyses

At harvest, roots, shoots and woody stems (*C. vulgaris*) were separated, oven-dried (60°C) for 24 h and finely ground before analysis. Following combustion in oxygen and helium (1000°C), the total N concentration was determined after reduction over copper and measurement of the reaction products by column chromatography (Carlo Erba Elemental Analyzer). Reduced nitrogen oxides were then led into a cryogenic trapping system (Finnigan MAT). Nitrogen was selectively absorbed on a molecular sieve at liquid nitrogen temperature and was later released from the sieve by heating to 80°C. The nitrogen gas then entered a mass spectrometer (Finnigan MAT 251 gas isotope ratio) through a capillary. Ions formed by electron bombardment of nitrogen gas in the spectrometer were separated electromagnetically and the intensities at mass 28 and mass 29 were measured simultaneously on fixed Faraday cups. Samples and references (KNO$_3$ and acetanilide) were alternatively measured and the reference gas was calibrated against atmospheric nitrogen (0·36630% labelled nitrogen). Analysis of atomic labelled nitrogen showed relative standard deviations of 0·02% for both samples.

Other subsamples of harvested plants were dry-ashed (600°C) after which concentrations of K, Ca, Mg and P were measured with an AutoAnalyzer (Technicon).

Differences in growth, nutrient uptake and allocation, and uptake of ^{15}N were compared with analysis of variance (Sokal & Rohlf 1981) after testing for homogeneity of variances, followed by a Student's *t*-test where necessary.

RESULTS

During the first 4 weeks of exposure to NH$_3$ *C. vulgaris* plants did not produce a significant amount of biomass (Table 1). However, after 9 weeks, the shoot production of *C. vulgaris* appeared to be increased in each treatment, although no differences occurred between treatment groups. The biomass of woody parts and roots had not significantly changed during the fumigation period of 9 weeks.

In contrast, *D. flexuosa* significantly increased its total biomass ($P < 0·05$) by 63–172% after 4 weeks of fumigation, depending on the treatment group examined (Table 2). The increase in biomass of *D. flexuosa* was due to increased root growth as well as shoot growth. After 9 weeks, both shoot and root production had again significantly increased

Table 1. Biomass production (g dry wt $\pm$ SE; $n = 10$) of *Calluna vulgaris* plants exposed to 100 μg m^{-3} NH$_3$. During the fumigation, one group of plants was sprayed with tap water three times weekly (+rain) and two groups were watered via the pot. At harvest, one of the last groups was rinsed for 30 s (+rinsed)

Period of exposure to NH$_3$ (weeks)	Treatment	Shoot	Wood	Root	Total
0		5·89±0·54	3·40±0·36	2·55±0·86	11·84±1·33
4	NH$_3$	5·52±0·37	3·11±0·40	3·02±0·77	11·65±1·08
	NH$_3$+rain	5·68±0·58	3·22±0·29	3·42±0·89	12·32±1·21
	NH$_3$+rinsed	5·94±0·38	3·23±0·40	2·45±0·54	11·62±1·10
9	NH$_3$	7·64±0·71	2·72±0·36	2·48±0·37	12·84±1·23
	NH$_3$+rain	7·81±0·76	3·30±0·44	2·50±0·25	13·61±1·16
	NH$_3$+rinsed	8·16±0·79	3·34±0·35	2·04±0·39	13·53±1·19

Table 2. Biomass production (g dry wt $\pm$ SE; $n = 10$) of *Deschampsia flexuosa* plants exposed to 100 μg m^{-3} NH$_3$. During the fumigation, one group of plants was sprayed with tap water three times weekly (+rain) and two groups were watered via the pot. At harvest, one of the last groups was rinsed for 30 s (+rinsed)

Period of exposure to NH$_3$ (weeks)	Treatment	Shoot	Root	Total
0		1·17±0·22	0·22±0·03	1·39±0·24
4	NH$_3$	1·72±0·20	0·53±0·06	2·26±0·22
	NH$_3$+rain	2·02±0·22	0·51±0·09	2·53±0·26
	NH$_3$+rinsed	3·10±0·37	0·84±0·20	3·78±0·44
9	NH$_3$	2·69±0·33	0·71±0·07	3·40±0·38
	NH$_3$+rain	2·71±0·20	0·97±0·08	3·67±0·24
	NH$_3$+rinsed	2·30±0·27	0·69±0·08	2·98±0·34

from that at 4 weeks ($P < 0.05$), except in the rinsed treatment group. The biomass of *D. flexuosa* plants rinsed at harvest after 4 weeks fumigation, was significantly higher ($P < 0.01$) than in the other treatment groups. However, differences between treatments were not significant after 9 weeks.

The proportion of nitrogen in plant organs resulting from the foliar uptake of NH$_3$ is given in Table 3. While NH$_3$-nitrogen accounted for only 5–7% of the total nitrogen in leaves of *C. vulgaris* after 4 weeks, *D. flexuosa* had assimilated a relatively greater proportion of its total nitrogen content in the shoot as NH$_3$-nitrogen: 16–18%. After 9 weeks, the difference between the species became smaller, 12–20% and 27–30% NH$_3$-derived nitrogen in leaves of *C. vulgaris* and *D. flexuosa*, respectively. The contribution of NH$_3$-nitrogen to the nitrogen concentrations in woody parts and roots also differed. After 4

Table 3. Proportion of total N taken up as NH_3 (%) in organs/tissues of *Calluna vulgaris* and *Deschampsia flexuosa* fumigated with 100 µg m^{-3} NH_3. Means ± SE are given ($n = 10$). During the fumigation, one group of plants was sprayed with tap water three times weekly (+rain) and two groups were watered via the pot. At harvest, one of the last groups was rinsed for 30 s (+rinsed)

| Period of exposure to NH_3 (weeks)	Treatment	Shoot	Wood	Root
C. vulgaris				
4	NH_3	4·9 ± 1·0	0·6 ± 0·4	0 ± 0·4
	NH_3 + rain	5·8 ± 0·8	1·8 ± 0·3	0 ± 0·4
	NH_3 + rinsed	7·1 ± 0·9	1·8 ± 0·8	0·4 ± 0·4
9	NH_3	19·6 ± 3·5	7·7 ± 1·9	4·3 ± 1·4
	NH_3 + rain	12·1 ± 1·5	4·8 ± 0·4	2·3 ± 0·6
	NH_3 + rinsed	16·3 ± 2·0	5·0 ± 0·6	3·3 ± 1·0
D. flexuosa				
4	NH_3	16·4 ± 1·1	—	7·8 ± 1·0
	NH_3 + rain	16·5 ± 1·1	—	10·5 ± 1·0
	NH_3 + rinsed	18·4 ± 1·0	—	7·5 ± 0·9
9	NH_3	26·9 ± 1·5	—	13·3 ± 1·0
	NH_3 + rain	28·9 ± 1·8	—	13·0 ± 1·2
	NH_3 + rinsed	29·8 ± 1·8	—	15·2 ± 1·2

weeks, fractions of NH_3-derived nitrogen were 7·5–10·5% in roots of *D. flexuosa* and less than 2% in roots or woody parts of *C. vulgaris*. After 9 weeks, these proportions had increased to 13–15% in roots of *D. flexuosa* and to 2–4% and 5–8% in roots and woody parts of *C. vulgaris*, respectively.

Neither the total nitrogen nor the labelled nitrogen fraction in the shoots of either species differed significantly between treatments (Table 4), although the total nitrogen content in the *C. vulgaris* group rinsed at harvest appeared to be lower than in the other groups after 4 weeks. The duration of exposure to ammonia did not significantly affect the mean nitrogen content, only the nitrogen concentration, indicating dilution due to plant growth. Thus, NH_3-nitrogen did not appear to be adsorbed to the leaf surface of *C. vulgaris* or *D. flexuosa*. The single rinsing of shoots at harvest or the regular spraying with tap water during the experiment apparently did not remove nitrogen either. Therefore, for the following calculations the data of the control and sprayed treatment groups were pooled.

Not all the NH_3-nitrogen taken up, however, was found in shoots of *C. vulgaris* and *D. flexuosa*, although the amount of labelled nitrogen measured in the roots of both species, especially *C. vulgaris*, was much lower. The treatment group sprayed with tap water from above did not show significantly more labelled nitrogen in the roots of either species than did the other two groups which were given water in the tray only. Therefore, it did not seem likely that NH_3 deposited to the soil was actually taken up by the roots, but was allocated to the woody parts and roots from the leaves. The amount of nitrogen allocated from the shoots to other organs differed considerably between the two species. While *C. vulgaris* had allocated less than 0·02 mg NH_3-nitrogen per gram wood or root after 4 weeks, *D. flexuosa* had already allocated 0·91 mg, a factor 45 higher (Fig. 1). At the final

Table 4. Effect of fumigation with $100 \, \mu g \, m^{-3} \, NH_3$ total-nitrogen, labelled-nitrogen content and nitrogen concentrations in shoots of *Calluna vulgaris* and *Deschampsia flexuosa*. Means $\pm$ SE are given ($n = 5$–10).During the fumigation, one group of plants was sprayed with tap water three times weekly (+rain) and two groups were watered via the pot. At harvest, one of the last groups was rinsed for 30 s (+ rinsed)

Period of exposure to NH_3 (weeks)	Treatment	N-total (mg)	^{15}N-total (mg)	N total (percentage dry wt)
C. vulgaris				
4	NH_3	106 ± 12	0.39 ± 0.05	2.00 ± 0.09
	$NH_3 +$ rain	113 ± 11	0.42 ± 0.04	1.94 ± 0.11
	$NH_3 +$ rinsed	89 ± 6	0.33 ± 0.02	1.50 ± 0.05
9	NH_3	116 ± 11	0.44 ± 0.04	1.51 ± 0.09
	$NH_3 +$ rain	111 ± 13	0.42 ± 0.05	1.76 ± 0.06
	$NH_3 +$ rinsed	100 ± 11	0.39 ± 0.04	1.27 ± 0.08
D. flexuosa				
4	NH_3	33 ± 6	0.12 ± 0.02	1.89 ± 0.09
	$NH_3 +$ rain	41 ± 5	0.16 ± 0.02	1.97 ± 0.12
	$NH_3 +$ rinsed	—	—	—
9	NH_3	44 ± 10	0.17 ± 0.04	1.52 ± 0.09
	$NH_3 +$ rain	42 ± 3	0.16 ± 0.01	1.65 ± 0.08
	$NH_3 +$ rinsed	—	—	—
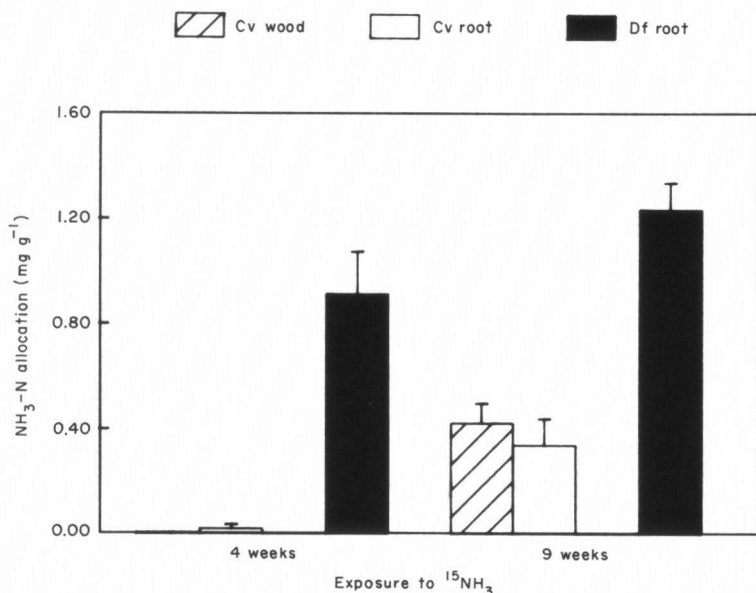
Fig. 1. Amount of NH_3-nitrogen allocated to woody parts and roots of *Calluna vulgaris* (Cv) and roots of *Deschampsia flexuosa* (Df) per unit organ dry weight (mg g^{-1}) following exposure to $100 \, \mu g \, m^{-3}$ labelled NH_3 for 4 and 9 weeks. Bars indicate SE ($n = 10$).
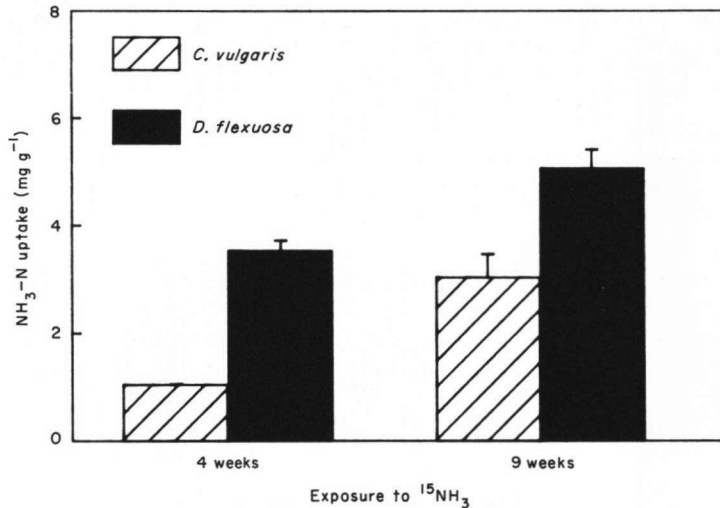
Fig. 2. Total uptake of NH_3-nitrogen per unit shoot weight (mg g^{-1}) of *Calluna vulgaris* and *Deschampsia flexuosa* following exposure to 100 µg m^{-3} labelled NH_3 for 4 and 9 weeks. Bars indicate SE ($n = 10$).

harvest however, *C. vulgaris* had allocated 0·42 and 0·34 mg NH_3-nitrogen g^{-1} to woody parts and roots, respectively, while *D. flexuosa* had allocated 1·23 mg NH_3-nitrogen g^{-1} to its roots, more than a factor three higher. Assuming NH_3 uptake via the shoot only, the amount of labelled nitrogen taken up per unit shoot weight was calculated for both species. Figure 2 shows that *D. flexuosa* took up significantly more NH_3 per unit shoot weight than *C. vulgaris* during the first 4 weeks ($P < 0·001$) as well as during the whole experimental period ($P < 0·01$).

There appeared to be no effect of regular spraying with tap water on the mineral composition of *C. vulgaris* or *D. flexuosa* (Table 5). After 9 weeks fumigation and spraying, only the phosphorus concentration in shoots ($P < 0·05$) and potassium concentration in roots ($P < 0·01$) of *D. flexuosa* were significantly different between treatments. Because there was no significant difference between the amount of labelled nitrogen in shoots of *C. vulgaris* between all three treatment groups and of *D. flexuosa* between the control and sprayed groups, the treatment group rinsed singly at harvest was not further analysed for the other nutrient concentrations.

DISCUSSION

One of the aims of this study was to determine if plants exposed only to dry deposition of NH_y adsorb nitrogen through the leaf surface. In addition, the influence of regular spraying with water on the eventual leaching of cations or cation exchange as suggested by Bobbink *et al.* (1990) was examined. Our data suggest that the answer to both questions with respect to this experiment is negative. When rinsed singly at harvest, leaves of *C. vulgaris* did indeed have less total nitrogen than non-rinsed plants after 4 weeks fumigation, although the amount was not statistically significant. Also, the amount of NH_3 taken up during the experiment (^{15}N) did not differ significantly between treatments, suggesting that rinsing had no effect. The lower nitrogen concentration in shoots of the rinsed *C. vulgaris* group, after both 4 and 9 weeks may be due to the higher biomass and thus to

Table 5. Mineral nutrient concentrations ($mg\ g^{-1}$) in *Calluna vulgaris* and *Deschampsia flexuosa* fumigated for 9 weeks with $100\ \mu g\ m^{-3}\ NH_3$. One group of plants was sprayed with tap water three times weekly (+rain). Means ± SE are given ($n = 10$) and *denotes a significant difference from the control at $P < 0.05$

Tissue/ organ	Treatment	P	K	Ca	Mg
C. vulgaris					
Shoot	NH_3	0·73±0·13	3·91±0·25	4·64±0·39	1·83±0·12
	NH_3+rain	0·83±0·08	4·67±0·36	5·49±0·51	1·80±0·17
Wood	NH_3	0·42±0·02	1·94±0·14	1·74±0·14	0·81±0·08
	NH_3+rain	0·34±0·03	2·14±0·14	1·84±0·15	0·88±0·14
Root	NH_3	0·60±0·05	1·34±0·14	2·48±0·37	0·86±0·10
	NH_3+rain	0·43±0·05	1·40±0·14	1·62±0·10	1·00±0·08
D. flexuosa					
Shoot	NH_3	1·15±0·11	9·41±0·71	2·06±0·08	1·52±0·10
	NH_3+rain	0·82±0·02*	8·26±0·75	2·44±0·20	1·42±0·07
Root	NH_3	0·74±0·05	1·45±0·09	1·46±0·08	0·35±0·05
	NH_3+rain	0·61±0·02	1·99±0·13*	1·47±0·17	0·37±0·03

some dilution of the nitrogen content. Neither the total nitrogen content nor the content of labelled nitrogen differed significantly between the control and the groups rinsed only at harvest or sprayed regularly with tap water. Therefore, either little or no nitrogen is adsorbed through the leaf surface, or spraying or rinsing had not rinsed adsorbed nitrogen from the leaves.

The data on the cation concentrations in this study do not indicate that the treatments applied in this experiment influenced the nutrient content in the leaves. A difference in the cation concentration between the control and sprayed treatment groups, where leaching might be of influence, was absent with the exception of the phosphorus concentration in *D. flexuosa*. However, concentrations of nutrients leached from leaves of *C. vulgaris* are likely to be too low to result in significant differences following a spraying treatment for a period of 9 weeks. For example, throughfall water measured each fortnight in the field under a canopy of *C. vulgaris* was found to have concentrations of 0·1 mmol l^{-1} potassium and 0·05 mmol l^{-1} for both magnesium and calcium, on an equivalent ionic basis (Bobbink *et al.* 1990). To leach significant amounts of nutrients, excessive rainfall, in the form of spraying would be necessary. The fact that no such differences were found in this experiment might also be influenced by the short duration of the spraying treatments (a matter of minutes leaving the shoots moist for 2–4 hours), with extensive dry periods in between. Throughfall water was not sampled and analysed, however, which might have provided more conclusive evidence on this.

The result of exposure to NH_3 in terms of nitrogen uptake and growth in this investigation was much more pronounced for *D. flexuosa* than for *C vulgaris*. *C. vulgaris* has a lower RGR (Heil 1984; Aerts 1989; Boot 1990) and has been found to respond more slowly to nitrogen fertilization than *D. flexuosa* (Dueck *et al.* 1990; Van der Eerden *et al.* 1990). With respect to the uptake of NH_3, an increase in photosynthetic capacity coincides with the growth of new leaves in early spring (Berdowski 1989), the period in which this

experiment took place. New leaves also have a higher photosynthetic capacity than 1-year-old leaves. Also, stomata at the leaf base of *C. vulgaris* are much less exposed than stomata on the leaf surface of *D. flexuosa* and thus have a higher boundary layer resistance, reducing the rate of gas exchange, and thus of NH_3 uptake in *C. vulgaris*.

As the nutrient availability increases, the root:shoot ratio generally decreases (Brouwer 1963). While the growth of *C. vulgaris* was primarily due to increased leaf biomass, *D. flexuosa* increased in its root biomass as well. A large root biomass in *D. flexuosa* may allow it to respond more rapidly when favourable conditions in heath vegetation present themselves, i.e. following the opening of the *Calluna* canopy, or re-growth in spring. It appears that *D. flexuosa* is also better able to retain its nitrogen at a higher RGR, implying higher nitrogen efficiency. Bobbink *et al.* (1990) found that after fertilization with $400 \, \mu\text{mol} \, l^{-1}$ ammonium sulphate every second week for 3 months, *C. vulgaris* had increased its biomass by a mere 5–8% while *D. flexuosa* had increased its biomass by 500%. On open nutrient-rich humus soils, given sufficient nitrogen and light conditions, a grass such as *D. flexuosa* will have a large competitive advantage, likely leading to the transition of *Calluna* heath to grass heath. On nutrient-poor sod-cut areas of heath however, *C. vulgaris* holds a competitive advantage (Heil 1984; Aerts 1989).

Increased nutrient availability has been found to alter competitive relationships in other species (Van den Bergh 1979; Berendse 1983). However, a closed canopy of *C. vulgaris* strongly filters NH_3 (Heil & Bruggink 1987; Heil *et al.* 1988; Bobbink *et al.* 1990), withholding both nitrogen and light from *D. flexuosa*. It is only following the opening of a *C. vulgaris* canopy by secondary stress factors such as drought, frost or heather beetle plagues that *D. flexuosa* might also benefit from foliar uptake of NH_3 or rapid mobilization of nitrogen from the litter and humus layer. While a factor such as drought allows little time for the reallocation of nitrogen, a stress factor such as a heather beetle plague allows even less, leaving *C. vulgaris* in nitrogen-polluted areas extremely vulnerable. This can be disastrous for *C. vulgaris* vegetation (Berdowski 1989), which appears to be an opportunistic species, retaining most of its nitrogen in its leaves for maximal photosynthesis.

Ammonia nitrogen appears to be taken up more rapidly at the leaf surface than ammonium or nitrate nitrogen taken up via the soil and roots (Van der Eerden *et al.* 1990). Although it was not clearly established in this study, circumstantial evidence was provided to support this. Usually, nitrogen taken up by the roots is quickly reallocated to the leaves, where it is incorporated in phostosynthetic enzymes such as Rubisco. However, at the first harvest, very little labelled nitrogen was measured in woody parts and roots, especially in *C. vulgaris*. Later, at the final harvest, much more ^{15}N was found in these organs. If nitrogen had been taken up via the roots and transported to the leaves, the opposite could be expected: initially higher ^{15}N concentrations in the root followed by dilution throughout the plant.

The assimilation and reallocation of NH_3-nitrogen occurs more rapidly in *D. flexuosa* than in *C. vulgaris*. After 4 weeks, *D. flexuosa* had reallocated nearly 40 times more atmospheric NH_3 to its roots than *C. vulgaris*. After 9 weeks exposure to NH_3, the relative difference in uptake and reallocation had decreased. At the last harvest *D. flexuosa* had accumulated approximately twice as much NH_3-nitrogen in total as had *C. vulgaris*.

When gaps are formed in *C. vulgaris* canopy due to drought, frost or insect herbivory (Berdowski 1989; Van der Eerden *et al.* 1990), *C. vulgaris* will likely be re-established in time under nutrient-poor conditions. Under richer soil conditions, or even under nutrient-poor conditions with high nitrogen depositions, the establishment of a grass heath is more

likely. Following the opening of a mature *C. vulgaris* canopy above a nitrogen-rich litter and humus layer (Van der Eerden *et al.* 1990), its rapid uptake and assimilation of nitrogen enables *D. flexuosa* to utilize both atmospheric and soil nitrogen for growth. Under these conditions, the growth rate of *D. flexuosa* during the first few weeks provides it with a competitive advantage. The result is that the heathlands in The Netherlands with high nitrogen concentrations are grass heaths rather than *Calluna* heaths.

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