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Exchange of trace gases between soils and the atmosphere in Scots pine forest ecosystems of the northeastern German lowlands

2. A novel approach to scale up N₂O- and NO-fluxes from forest soils by modeling their relationships to vegetation structure

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Abstract

Micro-scale emission rates of the primary and secondary relevant atmospheric greenhouse gases N₂O and NO from forest soils of northeast German Scots pine plantations are demonstrated to be highly dependent on the patterns of ground vegetation within the measuring chambers as well as on the canopy structure above the measuring plots. Based on an extensive statistical analysis of these dependencies, a model is developed allowing to predict N-trace gas emissions of different ecosystem types of mature Scots pine stands by applying an area-weighted averaging of local flux rates. The horizontal distribution patterns of emissions within the stands follow the small-scale distribution of N-deposition and precipitation controlled mainly by canopy structure. The mean emission rates of N₂O and NO are strongly dependent on top-soil state and vegetation—indicated by the vegetation type—and the atmospheric N-deposition. These findings open up the possibility to calculate N emissions from forest soils on a regional scale. Furthermore, the model predicts an increase of N₂O-emissions from forest soil with increasing thinning of stands. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: N-trace gas emissions; Scots pine forests; Vegetation types; Canopy structure; Small-scale variability; Upscaling

1. Introduction

Though there is growing information about the magnitude of trace gas exchange at the forest floor–atmosphere interface for a series of temperate forest sites (see compilation of data given in Butterbach-Bahl et al. (1997), Gasche and Papen (1999), and Papen and Butterbach-Bahl (1999)), the crucial problem of upscaling these fluxes from the microsite

(chambers) scale to larger forested areas remains unsolved so far. The upscaling is especially difficult, since the trace gas exchange between forest soils at a given site and the atmosphere shows huge variability in space (microsite variability) and time (seasonality) (e.g. Butterbach-Bahl et al., 2001). This microsite variability in trace gas fluxes is presumably in large parts due to microsite differences in the availability of N-substrate, water, and oxygen, as well as due to the competition between soil microorganisms and vegetation for substrates. On the other hand, ground vegetation has been proven to be a powerful indicator of differences in these parameters on a microsite level

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as well as on the level of entire forest ecosystems (Krüdener, 1903; Schönhar, 1954; Passarge and Hofmann, 1964; Ellenberg and Mueller-Dombois, 1967; Hofmann, 1968; Ellenberg et al., 1991). Different vegetation patterns are used to define different forest ecosystem types. Forest typologies have been developed for about 100 years (see compilation given by Jenssen (2001), and Migunova (2000)) and are the basis for standardized forest classification in several countries all over the world. This could be used for upscaling trace gas fluxes to regional scales via forest types provided that close relationships between microsite vegetation patterns and measured trace gas fluxes exist.

From 1995 to 1998, Butterbach-Bahl et al. (2001) carried out N-trace gas measurements in five Scots pine forest ecosystems of the northeastern German lowlands exposed to different levels of atmospheric N-input. These measurements were accompanied by a detailed analysis of vegetation structures at the measuring plots which will be presented in this paper. The first objective of the simultaneous investigations of N-trace gas fluxes and vegetation structures was to prove if differences in canopy structure and composition of ground vegetation can be used to explain microsite variability in trace gas fluxes. The second objective was to prove if dependencies between vegetation patterns and trace gas fluxes can be used for upscaling trace gas emissions from microsite levels to larger forested areas by models based on the forest typology approach.

2. Methods

The methods of trace gas measurements and the description of the five investigated Scots pine forest sites are presented in detail by Butterbach-Bahl et al. (2001). In the following, the methods used to identify relationships between vegetation patterns and trace gas emissions as well as the techniques of model development will be presented.

2.1. Determination of vegetation patterns at sites of trace gas measurements

The approach followed in this study was based on a comprehensive analysis of Scots pine (*Pinus sylvestris*

L.) forest vegetation in the northeast German lowlands by Hofmann (1969, 1997). The percent cover estimates of the occurring plant species were recorded on altogether 1500 sample plots in mature Scots pine forests. Each sample plot covers an area of at least the square of the tree height, e.g. an area of at least 400 m² for a tree height of 20 m. This area can be considered as minimal area of a forest ecosystem (Hofmann et al., 1999). The mean composition of vegetation for five Scots pine forest types which cover together about two-thirds of the woodlands of the northeast German lowlands is presented in Table 1.

Trace gas measurements were performed at five Scots pine forest sites (macrosites) of the northeast German lowlands with different atmospheric N-inputs. Measurements were carried out in form of field campaigns at different seasons during the years 1995–1998 (Butterbach-Bahl et al., 2001). During each campaign and at a certain macrosite, five NO-measuring chambers (0.25 m² area covered by each chamber) and five N₂O-measuring chambers (0.5 m² area covered by each chamber) were installed. The characteristic combination of plant species enclosed by the individual chambers corresponded to each one of the investigated vegetation types. Due to their small size, the individual measuring chambers (microsites) did never contain the full spectrum of species occurring on the minimum area of the corresponding vegetation type, but in every case most abundant species in their characteristic quantitative composition. Summarizing all the microsite vegetation plots belonging to a given vegetation type, we get a species composition similar to the mean composition of the corresponding vegetation type on minimum area which is presented in Table 1. However, the microsite plots belonging to a certain vegetation type were often located at more than one macrosite; and the different microsites at a given macrosite did not necessarily belong to the same vegetation type. In the result, we could derive results for a variety of different Scots pine vegetation types, some of them exposed to different levels of N-input.

After measuring the flux rates at the microsites, the canopy structure above each measuring chamber was identified. For this purpose, the canopy section in perpendicular projection above the measuring chambers was recorded by a camera with different zoom resolutions, thereby catching an area of canopy of up

Table 1

Average percent cover estimates of plant species in five widespread Scots pine forest vegetation types of the northeast German lowlands^{a,b}

Species	Forest vegetation type (percent cover)				
	<i>Avenello-Culto-Pinetum</i>	<i>Myrtillo-Culto-Pinetum</i>	<i>Calamagrostio-Culto-Pinetum</i>	<i>Rubo-Avenello-Culto-Pinetum</i>	<i>Rubo-Culto-Pinetum</i>
Tree layer					
<i>Betula pendula</i>		1	1	1	1
<i>Pinus sylvestris</i>	67	65	64	63	67
<i>Fagus sylvatica</i>		1		1	
<i>Sorbus aucuparia</i>					1
Shrub layer					
<i>Pinus sylvestris</i>	5	1		3	
<i>Sambucus nigra</i>					1
<i>Fagus sylvatica</i>		1			1
<i>Prunus serotina</i>				1	
<i>Quercus petraea</i>					1
<i>Quercus robur</i>		1		1	1
<i>Betula pendula</i>				4	
<i>Sorbus aucuparia</i>				1	1
<i>Frangula alnus</i>				1	2
<i>Rubus fruticosus</i> agg.				2	8
<i>Rubus idaeus</i>			4	10	46
Herb layer					
<i>Urtica dioica</i>			2		1
<i>Deschampsia cespitosa</i>					1
<i>Dryopteris dilatata</i>				1	2
<i>Oxalis acetosella</i>			1	2	15
<i>Carex hirta</i>				1	1
<i>Holcus lanatus</i>					1
<i>Impatiens parviflora</i>					2
<i>Moehringia trinervia</i>			1	1	1
<i>Brachypodium sylvaticum</i>					2
<i>Dactylis polygama</i>			1		1
<i>Epilobium angustifolium</i>			1	1	
<i>Senecio sylvaticus</i>	1				
<i>Avenella flexuosa</i>	41	22	10	47	11
<i>Carex pilulifera</i>	1				
<i>Melampyrum pratense</i>		1			
<i>Calamagrostis epigejos</i>	1	1	62	3	4
<i>Dryopteris carthusiana</i>			1	1	1
<i>Holcus mollis</i>				1	1
<i>Pteridium aquilinum</i>		3	1	4	4
<i>Vaccinium myrtillus</i>	1	49	2	1	1
<i>Vaccinium vitis-idaea</i>		1			
<i>Agrostis capillaris</i>	1		1	2	2
<i>Anthoxanthum odoratum</i>			1	2	1
<i>Festuca ovina</i>	2	1	3		
<i>Calluna vulgaris</i>	1	1			
Moss layer					
<i>Polytrichum formosum</i>					1
<i>Scleropodium purum</i>	2	8	10	20	23
<i>Dicranum scoparium</i>	1		1		
<i>Hypnum cupressiforme</i>	8	4	5		1
<i>Dicranum polysetum</i>	4	9		1	

Table 1 (Continued)

Species	Forest vegetation type (percent cover)				
	<i>Avenello-Culto-Pinetum</i>	<i>Myrtillo-Culto-Pinetum</i>	<i>Calamagrostio-Culto-Pinetum</i>	<i>Rubo-Avenello-Culto-Pinetum</i>	<i>Rubo-Culto-Pinetum</i>
<i>Pleurozium schreberi</i>	27	38	18	20	13
<i>Polytrichum juniperinum</i>	1				
<i>Ptilidium ciliare</i>		1			
Number of plots ^c	254	222	72	137	41
Average number of species per plot ^c	17	17	17	22	26

^a Percent cover estimates below 1% are not considered.

^b The bold-faced numbers denote the characteristic species composition distinguishing between different forest vegetation types.

^c Area of each plot at least 400 m², see Section 2.1.

to 150 m². Furthermore, the trees within that canopy area were classified according to their crown position as dominant, codominant, intermediate, and over-topped trees.

2.2. Statistical analysis of the relationships between local vegetation structures and NO and N₂O fluxes

Altogether, mean N₂O-fluxes from 127 microsites, mean NO-fluxes from 116 microsites, as well as the corresponding records of local vegetation type and canopy structure at these 243 microsites were used for the subsequent statistical analysis.

In order to consider both the influence of local vegetation type and of actual N-deposition level on microsite emissions, seven different strata were defined (Fig. 1). The local vegetation types classified to the *Myrtillo-Pinus*-type and to the *Rubus-Pinus*-type were found in mature Scots pine stands with a normal degree of canopy closure between 0.6 and 0.8 and mean N-deposition rates between 10 and 15 kg N ha⁻¹ per annum at forest floor. The local vegetation types classified to the *Calamagrostis-Pinus*-type were observed in thinned stands with a canopy closure between 0.4 and 0.6 and high deposition rates of 20–25 kg N ha⁻¹ per annum. The *Avenella-Pinus*-type and the *Rubus-Avenella-Pinus*-type were found both in closed and in thinned stands, and at both N-deposition levels. After this stratification, the *H*-test according to Kruskal and Wallis (1952) was applied in order to prove whether the seven samples have the same statistical mean of N-trace gas fluxes or not. In addition, the *U*-test according to Wilcoxon, Mann, and Whitney (Mann and Whitney, 1947) was used to

identify differences in the magnitude of N-trace gas fluxes between the different strata.

N- and water-inputs on forest floor are known to vary with canopy structure at distances of few meters only (Kreutzer, 1985; Wilpert, 1994; Wilpert et al., 1996; Jenssen, 1996a,b, 1997; Böttcher et al., 1997). In order to consider the effect of these small-scale variations, the canopy records above measuring chambers were analyzed. From a first data analysis, it turned out that measuring chambers in the vicinity of dominant trees frequently yielded positive and negative extreme values of N-trace gas emissions. The same appeared if the tree above the chamber was neighbored by a large canopy gap in the main wind direction. Further statistical analysis revealed the necessity to define eight different strata of local canopy structure (Fig. 1) to describe the effects of N- and water-input variations on a microsite level. The N-trace gas flux data were assigned to these eight strata and were tested with respect to statistical significance by the *H*-test again.

2.3. Modeling of micro-scale emission rates from local vegetation structures

After the relevant structural determinants of N-trace gas emissions had been determined at a microsite scale, a model was developed describing differences both in vegetation and deposition types ($i = 1, \dots, 7$) as well as in canopy structures ($j = 1, \dots, 8$)

$$y_{i,j} = y_i(1 + f_j), \quad i = 1, \dots, 7, \quad j = 1, \dots, 8 \quad (1)$$

The parameters y_i model specific flux rates for the seven distinguished vegetation and N-deposition types

Atmospheric N-deposition / Canopy structure

		Moderate deposition rates (10 – 15 kg N ha ⁻¹ a ⁻¹)				High deposition rates (20 – 25 kg N ha ⁻¹ a ⁻¹)									
		Closed canopy (degree of canopy closure = 0.6 - 0.8)				Thinned canopy (degree of canopy closure = 0.4 - 0.6)									
Atmospheric exposure of trees above the measuring chambers	High atmospheric exposure (Tree is dominant within the canopy or a large gap can be found in the main wind direction)	3		1		3		1		4	10	1	Canopy gap (j = 1)		
		5		0		4		2		3	12	1	Crown edge in windward (j = 2)		
		7		3		2		0		1	1	3	Crown center (j = 3)		
		5		1		1		1		0	3	0			
	4		0		3		2		1	6	3	Crown edge at lee side (j = 4)			
	5		1		4		1		0	2	7				
	3		0		2		0		2	4	1	Canopy gap (j = 5)			
	2		1		3		0		1	5	2				
	Low atmospheric exposure (Tree is not dominant within the canopy and no large gap can be found in the main wind direction)	0		0		2		1		0	1	0	Crown edge in windward (j = 6)		
		2		4		8		1		0	1	0	Crown center (j = 7)		
		2		1		4		0		0	2	0			
		2		1		6		0		1	5	0			
	4		1		5		0		1	3	1	Crown edge at lee side (j = 8)			
	4		1		1		0		0	0	1				
	4		2		9		0		0	1	1				
	5		1		7		0		0	3	1				
		<i>Myrtillus-Pinus</i> -Type (i = 1)		<i>Avenella-Pinus</i> -Type (i = 2)		<i>Rubus-Avenella-P.</i> -Type (i = 3)		<i>Rubus-Pinus</i> -Type (i = 4)		<i>Avenella-Pinus</i> -Type (i = 5)		<i>Rubus-Avenella-P.</i> -Type (i = 6)		<i>Calamagrostis-P.</i> -Type (i = 7)	
		Local vegetation type													

Canopy structure in perpendicular projection above the measuring chambers

Fig. 1. Total number of chamber sites with NO measurements (above value) and N₂O measurements (below value) stratified according to differences in local vegetation types, actual atmospheric N-deposition ($i = 1, \dots, 7$) and canopy strata ($j = 1, \dots, 8$).

modified by the eight parameters f_j in dependence on canopy structure. The altogether 15 parameters of the model were estimated by a least-squares fit. For minimization of the sum of deviation squares we used the downhill simplex method in multidimensions according to Nelder and Mead implemented in the routine AMOEBA of numerical recipes (Press et al., 1992).

2.4. Upscaling N-trace gas fluxes to ecosystem level

Mean emission rates of NO and N₂O can be derived on the macro-scale of ecosystems, provided that information on the different strata used in Eq. (1) is accessible on larger scales. In order to get reliable information about the distribution of different canopy strata in forest stands, about 700 randomly chosen

Table 2

Relative frequencies $n_j^{(k)}$ of different canopy strata^a for mature Scots pine forests in the northeastern German lowlands

	Canopy strata								$\sum_{j=1}^8 n_j^{(k)}$
	$n_1^{(k)}$	$n_2^{(k)}$	$n_3^{(k)}$	$n_4^{(k)}$	$n_5^{(k)}$	$n_6^{(k)}$	$n_7^{(k)}$	$n_8^{(k)}$	
Closed stand ^b ($k = 1$)	0.09	0.09	0.13	0.07	0.12	0.12	0.20	0.18	1.0
Thinned stand ^c ($k = 2$)	0.32	0.11	0.22	0.13	0.03	0.06	0.06	0.07	1.0

^a Canopy strata ($j = 1, \dots, 8$) as defined in Fig. 1.^b Degree of canopy closure 0.6–0.8.^c Degree of canopy closure 0.4–0.6.

samples of local canopy structures were analyzed according to the method explained in Section 2.1 and subsequently classified according to the strata defined in Fig. 1. In the result, relative frequencies $n_j^{(k)}$ were calculated for the eight canopy strata (Table 2). The relative frequencies $n_j^{(k)}$ for closed ($k = 1$) and thinned ($k = 2$) stands as well as the parameters y_i and f_j obtained from the fitting of Eq. (1) were used to calculate mean emission rates for seven types of ecosystems at a certain deposition level, each for two types of canopy closure

$$\overline{y_i^{(k)}} = y_i \sum_{j=1}^8 n_j^{(k)} (1 + f_j), \quad k = 1, 2, \quad i = 1, \dots, 7 \quad (2)$$

We stress that possible ambiguities in defining different canopy strata are irrelevant after this syntheses of microsite information on macrosite level, because both classification of canopy structures above measuring chambers and the determination of relative frequencies $n_j^{(k)}$ (Table 2) were carried out by the same person. The confidence intervals of the mean values yielded by Eq. (2) were calculated from the errors of model parameters obtained from Eq. (1) according to the rules of error propagation.

3. Results and discussion

3.1. Micro-scale determinants of NO- and N₂O-emissions in Scots pine forests

The statistical hypotheses, that the NO- and N₂O-emission rates belonging to the seven defined vegetation/deposition types have the same mean value, was

rejected on a $P < 0.001$ level of significance. In particular, the mutual comparison in pairs of each two of the seven sample groups yielded significant ($P < 0.05$) differences for all the 21 pairs of strata for NO, and for 20 of the 21 pairs for N₂O. This result clearly verifies that ground vegetation can be used as a powerful indicator for the magnitude of NO- and N₂O-trace gas fluxes from forest soils at a given level of actual N-input. Furthermore, the results show the importance of the actual level of N inputs for the amount of emissions, because each the *Avenella-Pinus*-type and the *Rubus-Avenella-Pinus*-type are significantly distinguished at different levels of deposition height with respect to the NO- and N₂O-emission rates.

On the other hand, there are highly significant differences for the microsite flux rates of NO ($P < 0.05$) and N₂O ($P < 0.01$) emitted under different canopy strata. This result confirms the hypothesis that the canopy structure is an important regulator for the magnitude of N-trace gas fluxes.

Thus, the choice of the model variables in Eq. (1) including vegetation strata as well as different canopy strata is fully justified. Eq. (1) explains about 40% of the variance of microsite variability in NO-fluxes and about 30% of the variability in N₂O-fluxes. The analysis of model residuals showed a relatively even scattering versus the considered strata (vegetation and canopy). Presumably, a large part of this scattering can be attributed to seasonal influences on N-trace gas fluxes which have been neglected at this stage of model development. This is justified by the large number of field measurements, which were performed evenly distributed over the different seasons of the years 1995–1998 (Butterbach-Bahl et al., 2001) However, some of the local vegetation types defined in

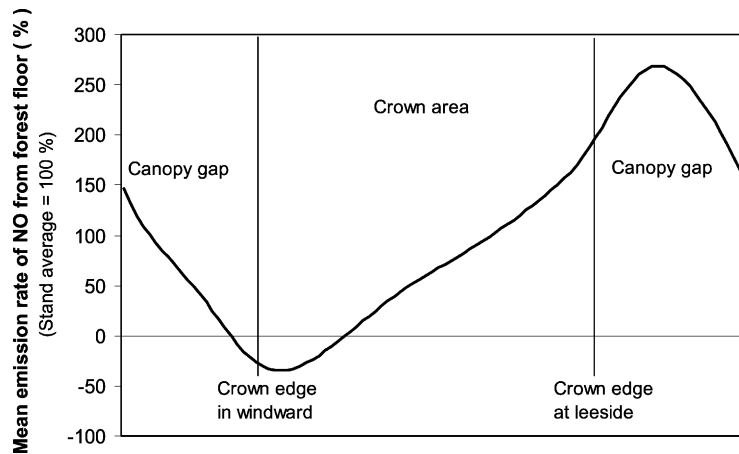


Fig. 2. Mean NO-emission pattern on forest floor in mature Scots pine plantations of the northeast German lowlands (intersection from WSW to ENE). The flux rate is given as percentage of the characteristic mean value of the corresponding stand (cf. Table 3).

Fig. 1 were represented by only few datasets which might cause bias to the results. Thus, meteorological data need to be considered in future work for derivation of representative annual flux rates.

3.2. The horizontal distribution of N-trace gas emissions on forest floor

The mean NO-emission pattern on forest floor depicted in Fig. 2 shows a distinct systematic variation in dependence on the canopy structure above. Under crown edges in windward direction, even a slight net deposition is prevailing. On the other hand, the net emissions on lee-side crown edges are raised by a factor of 2.5 compared to stand average. This distribution pattern—which is most distinct for dominate trees—is in excellent agreement with results obtained in other studies. Jenssen (1996a,b) showed that turbulent mass transport within Scots pine canopies leads to a redistribution of precipitation particles towards lee-side crown edges. This effect is increased with increasing wind velocity, decreasing mass of transported particles, and decreasing canopy closure. Deposition measurements of Böttcher et al. (1997) confirmed the existence of spatial deposition patterns of atmagenic inputs on forest floor following canopy structure. On the other hand, Fenn et al. (1996), Davidson and Kinglerlee (1997), Gasche and Papen (1999), and Butterbach-Bahl et al. (2001) have shown a positive correlation between the magnitude of NO-fluxes

and the amount of N-deposition for different temperate forest ecosystems. Obviously, the emission pattern shown in Fig. 2 confirms this close relationship between the rates of N-deposition and NO-emission on a microsite scale.

Compared to the NO-fluxes, the spatial distribution of N₂O-emissions on a microsite scale is less distinct, but in general agreement with the spatial distribution of NO-fluxes (Fig. 3). The trend of a shift of N₂O-fluxes to the direction of the crown center can be most likely attributed to the spatial distribution of water-input below pine canopies. As can be seen from a comparison with the horizontal distribution pattern of rainfall (Fig. 4), the maximal N₂O-emissions seem to be shifted towards the regions of forest floor with better water supply. However, a better water supply of forest soil is likely to increase denitrification activity, which may lead to a shift of the N₂O/NO ratio towards N₂O (Firestone and Davidson, 1989; Davidson, 1993).

3.3. N-trace gas fluxes for Scots pine forest ecosystems in dependence on vegetation type, magnitude of N-deposition, and degree of canopy closure

The highly significant ($P < 0.001$) relation between N-trace gas emissions and patterns of ground vegetation on a microsite scale allows to transfer the obtained results from the microsite level to the ecosystem level. Using Eq. (2), mean N-trace gas emission rates for five

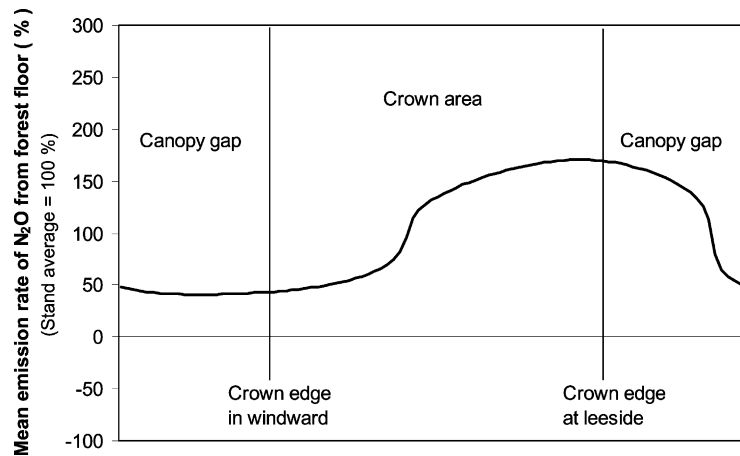


Fig. 3. Mean N_2O -emission pattern on forest floor in mature Scots pine plantations of the northeast German lowlands (intersection from WSW to ENE). The flux rate is given as percentage of the characteristic mean value of the corresponding stand (cf. Table 3).

widespread Scots pine ecosystem types of the northeast German lowlands exposed to different levels of N-deposition were calculated (Table 3). Different vegetation types, as well as the same types with different N-inputs, are clearly distinguished from each other. The large confidence interval of the *Rubus-Pinus*-type is due to the low number of chamber sites belonging to this vegetation type (see Fig. 1).

The investigated Scots pine vegetation types represent an ecological series distinguished mainly by the nutritional status of the soil. The following

interpretation of the results presented in Table 3 can be given within the context of previous findings:

1. The NO -emissions as well as the sum of NO - and N_2O -emissions clearly increased with increasing trophic status of the top-soil at a certain level of atmospheric N-input. The increase of the trophic state of top-soil corresponds to an improvement in humus quality (raw-humus in the *Avenello*- and the *Myrtillo-Culto-Pinetum*, raw-humus like moder in the *Calamagrostio-Culto*- and in the

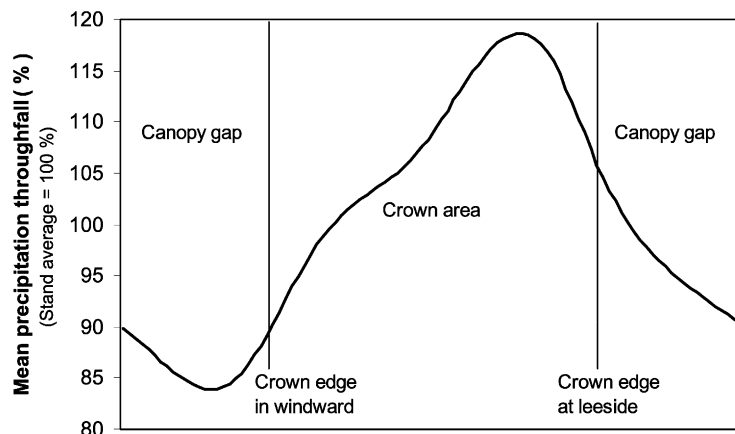


Fig. 4. Mean distribution pattern of below-canopy precipitation in mature Scots pine plantations of the northeast German lowlands (intersection from W to E) during the growing season (May to September) 1993.

Table 3
Mean NO- and N₂O-emission rates (April to November) and the corresponding confidence limits ($P < 0.05$) on forest floor of different Scots pine forest ecosystems of the northeast German lowlands

Actual vegetation type	Trophic state of top-soil	Level of N-input with throughfall							
		Moderate ^a (10–15 kg N ha ⁻¹ per annum)				High ^b (20–25 kg N ha ⁻¹ per annum)			
		NO (μg NO- N m ⁻² h ⁻¹)	N ₂ O (μg N ₂ O- N m ⁻² h ⁻¹)	NO + N ₂ O (μg N m ⁻² h ⁻¹)	N ₂ O/ NO	NO (μg NO- N m ⁻² h ⁻¹)	N ₂ O (μg N ₂ O- N m ⁻² h ⁻¹)	NO + N ₂ O (μg N m ⁻² h ⁻¹)	N ₂ O/ NO
<i>Myrtillo-Culto-Pinetum</i>	Oligo- to mesotrophic	4.4 ± 0.9	3.5 ± 0.7	7.9 ± 1.5	0.8				
<i>Avenello-Culto-Pinetum</i>	Oligo- to mesotrophic	0.4 ± 0.2	10.3 ± 3.6	10.7 ± 3.8	26	9.5 ± 3.5	15.0 ± 7.4	25 ± 11	1.6
<i>Calamagrostio-Culto-Pinetum</i>	Mesotrophic					39 ± 17	34.0 ± 7.6	73 ± 24	0.9
<i>Rubo-Avenello-Culto-Pinetum</i>	Meso- to eutrophic	7.7 ± 1.8	8.6 ± 1.4	16.3 ± 2.2	1.1	49 ± 10	20.2 ± 2.9	69 ± 13	0.4
<i>Rubo-Culto-Pinetum</i>	Eutrophic	15 ± 19	6.3 ± 3.1	22 ± 22	0.4				

^a For the stands with moderate N-input a degree of canopy closure between 0.6 and 0.8 was assumed.

^b For the stands with high N-input a degree of canopy closure between 0.4 and 0.6 was assumed.

Rubo-Avenello-Pinetum, and moder in the *Rubo-Culto-Pinetum*). The NO-emissions, but also a large amount of the N₂O-emissions, are the result of nitrification processes (e.g. Firestone and Davidson, 1989; Papen and Butterbach-Bahl, 1999; Gasche and Papen, 1999). The importance of nitrification as the primary source of NO and N₂O at the Scots pine forest sites in the north-eastern German lowlands is further supported by results obtained by Papen et al. (1999) who showed that cell numbers of heterotrophic nitrifiers increased within this ecological series. Autotrophic ammonia oxidizers, which are known to be able of NO- and N₂O-production, could never be detected in these acid soils (Papen et al., 1999). Therefore, we assume that the increases in NO-emissions and total N-trace gas emissions are most likely due to increased heterotrophic nitrification activity with increasing trophic status.

2. For a given ecosystem type and, hence, comparable humus quality, the emissions of both trace gases increase with the amount of N-deposition. This mainly concerns NO, whereas the N₂O/NO-ratio decreases with increasing deposition (Table 3). This agrees with the results of Papen et al. (1999) who found an increase of aerobic heterotrophic nitrifiers, but a decrease of denitrifiers with increasing N-deposition.
3. For comparable N-deposition and humus quality, the N₂O/NO-ratio markedly increased with the degree of coverage by grasses as compared to that of shrubby vegetation (Table 4). A final explanation of this observation cannot be given at present. However, it can be hypothesized that the relatively dense and hydrophobic raw-humus of grass forests is less aerated, which could enhance denitrification processes and therefore increase the N₂O/NO-ratio in grass forests. Probably, also the different uptake of NH₄⁺- and NO₃⁻-ions by the roots of the plants could have an important influence on

the nitrification and denitrification processes. However, this question remains open for further investigation.

The results summarized in Table 3 were calculated assuming a normally closed canopy (degree of canopy closure between 0.6 and 0.8) for moderate N-inputs, but a degree of canopy closure between 0.4 and 0.6 for stands with a high N-input. This assumption holds not only for the forest sites investigated experimentally in our study, but seems to be reasonable also with respect to a regionalization of our data, because longstanding high N-depositions have lead to a thinning of forest stands due to an enhanced tree mortality (Hofmann, 1996). However, a strong thinning of forest canopies can be carried out, e.g. in order to prepare an understory of deciduous trees. In order to assess the implications of this management action with respect to N-trace gas emissions, we predicted also mean emission rates for strongly thinned stands ($k = 2$ in Eq. (2)) with a moderate level of N-deposition, though they had not been investigated in the field experiments. According to the model results presented in Fig. 5, the thinning induces a slight increase of the N-trace gas emissions from forest soils. This increase is due to an increase of N₂O-emissions, whereas NO-emissions are unchanged or even slightly diminished. This means that thinning in particular favors a widening of the N₂O/NO-ratio. These model results are in agreement with the above interpretations, because thinning improves N-substrate availability due to enhanced mineralization. Furthermore, the assumed reduction of canopy cover from about 0.7 to about 0.5 leads to an increase of annual precipitation throughfall of 10–15% (Janssen, 1997) which could support denitrification processes inducing an enhanced N₂O-production. However, the establishment of a deciduous understory will change the ecology of Scots pine forests completely. At the present stage of investigations, we cannot make any prediction of N-trace gas

Table 4
Comparison of shrubby and grass pine forests with respect to their N₂O/NO-ratio

Vegetation types in pairs	N ₂ O/NO-ratio in pairs
<i>Myrtillo-Avenello-Culto-Pinetum</i> with moderate N-input	0.8/26
<i>Rubo-Rubo-Avenello-Culto-Pinetum</i> with moderate N-input	0.5/1.1
<i>Rubo-Avenello-Calamagrostio-Culto-Pinetum</i> with high N-input	0.4/0.9

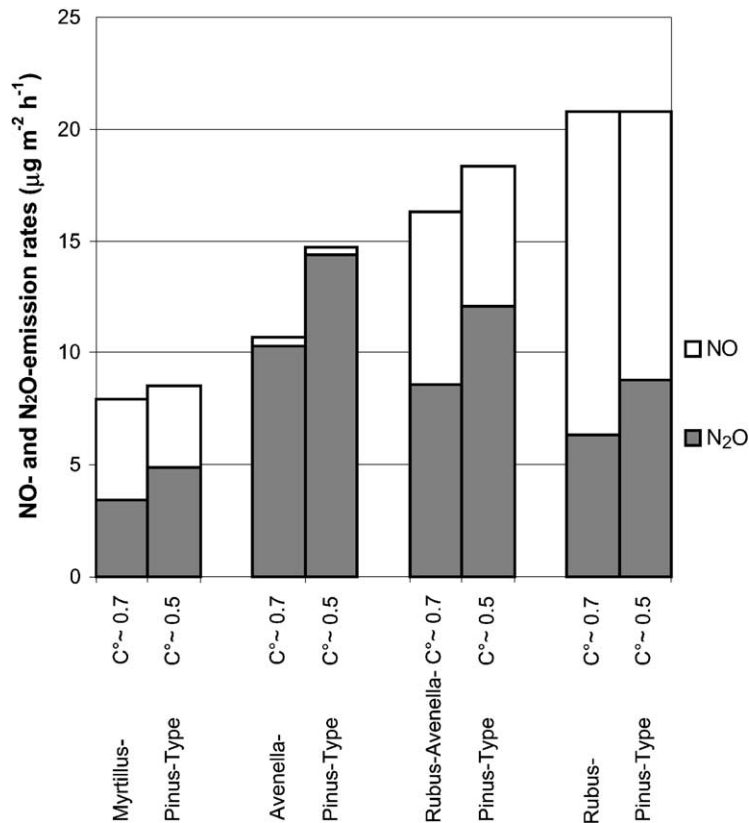


Fig. 5. The influence of strong thinning of mature Scots pine stands on the mean NO- and N₂O-emission rates for a series of forest types exposed to moderate N-deposition. For each forest type, the left column denotes the emission rates for normally closed canopies (degree of canopy cover $C^\circ = 0.6\text{--}0.8$), and the right column the emission rates after strong thinning (degree of canopy closure $C^\circ = 0.4\text{--}0.6$).

emissions for the process of conversion of Scots pine forest plantations into mixed stands with a deciduous understory.

4. Conclusions

The study revealed the high indicator value of vegetation for the emission of N₂O and NO from forest soils of Scots pine forests. The close relationships on microsite level were used to upscale emissions of the two trace gases for a variety of Scots pine forest ecosystems exposed to different atmospheric N-loads. The investigated Scots pine forest types cover about two-thirds of the woodlands of the northeast German lowlands. Consequently, the results presented in this paper can be used for a quantification of N₂O- and

NO-emissions for the overwhelming part of the woodlands of the region, i.e. for about 13,000 km² of actual temperate forest area (Hofmann, 1996). However, in order to give reliable annual flux rates, we have to consider the annual course of N-trace gas emission explicitly. In a forthcoming paper, we will incorporate meteorological data into our models in order to calculate annual fluxes which are representative for the considered forest types. The aim of the present study was mainly to demonstrate the principal feasibility of a novel upscaling approach based on the enormous indicator value of vegetation.

Forest policy is directed to a large-scale replacement of the artificial Scots pine plantations covering about 70% of the woodlands of the northeast German lowlands presently by mixed forests including a considerable part of deciduous trees. In order to

support forest-political and silvicultural decisions, there is an urgent need to predict the implications of different replacement scenarios with respect to the development of N-trace gas emissions. These predictions which are indispensable for a comprehensive assessment of forest sustainability require further studies in forests composed of various kinds of tree species.

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