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Mass loss and nitrogen dynamics in decomposing acid forest litter in the Netherlands at increased nitrogen deposition

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Abstract. Litterbag experiments were carried out in five forest ecosystems in the Netherlands to study weight loss and nitrogen dynamics during the first two years of decomposition of leaf and needle litter. All forests were characterized by a relatively high atmospheric nitrogen input by throughfall, ranging from 22—55 kg N ha^{-1} yr^{-1}.

Correlation analysis of all seven leaf and needle litters revealed no significant relation between the measured litter quality indices (nitrogen and lignin concentration, lignin-to-nitrogen ratio) and the decomposition rate. A significant linear relation was found between initial lignin-to-nitrogen ratio and critical nitrogen concentration, suggesting an effect of litter quality on nitrogen dynamics.

Comparison of the decomposition of oak leaves in a nitrogen-limited and a nitrogen-saturated forest suggested an increased nitrogen availability. The differences in capacities to retain atmospheric nitrogen inputs between these two sites could be explained by differences in net nitrogen immobilization in first year decomposing oak leaves: in the nitrogen-limited oak forest a major part (55%) of the nitrogen input by throughfall was immobilized in the first year oak leaf litter.

The three coniferous forests consisted of two monocultures of Douglas fir and a mixed stand of Douglas fir and Scots pine. Despite comparable litter quality in the Douglas fir needles in all sites, completely different nitrogen dynamics were found.

Introduction

Increasing atmospheric nitrogen deposition has a large impact on ecosystem functioning in the northern temperate forests. Originally these forests were nitrogen-limited, but the large amount of nitrogen deposited each year by atmospheric deposition has led to nitrogen saturation in many areas (Hauhs et al. 1989; Van Breemen & Verstraten 1991).

An ecosystem shows nitrogen saturation when the nitrogen input exceeds the capacity of biota to retain the nitrogen input (Aber et al. 1989). Soil organic matter can act as an important sink for the increased supply of nitrogen. The dynamics of soil organic matter are determined by aboveground and belowground litter production and output via decomposition. Litter production is expected to increase with increased nitrogen supply in a nitrogen-limited forest ecoysystem, until another environmental factor becomes limiting to growth. Root turnover may either increase (Aber et al. 1985) or decrease (Vogt et al. 1990) as a result of an increased nitrogen supply. The effect of an external nitrogen supply on the decomposition rate is not clear. Although the traditional concept of a (critical) C-to-N ratio determining the microbial activity involves a period of nitrogen limitation (Parnas 1975), a literature survey carried out by Fog (1988) demonstrated that added nitrogen often has no effect or a negative effect on microbial activity. A negative effect is often found with recalcitrant organic matter, whereas no effect by added nitrogen is common for easily degradable organic material.

In the Netherlands, many forest soils receive large amounts of atmospheric NH_4^+ via dry and wet deposition (Van Breemen et al. 1982; 1987), ranging from 20 to 80 kg N ha^{-1} yr^{-1} (Heij & Schneider 1991). Differences in nitrogen inputs exist due to local factors like distance from and exposure to the agricultural sources (Van Breemen & Verstraten 1991). In order to study the effect of increased nitrogen input on decomposition, litterbag experiments were carried out in five forest ecosystems with different nitrogen deposition rates. In this paper, the results for decomposition rates and for nitrogen dynamics in the decomposing litter are reported. In addition, the results are compared with the traditional theories on litter decomposition, which are primarily based on studies in nitrogen limited forests.

Material and methods

Forest sites

The decomposition experiments were carried out in three coniferous and two deciduous forest ecosystems in the Netherlands. Four sites (Leuvenum, Speuld, Kootwijk and Buunderkamp) are located in the Veluwe region in the central part of the Netherlands. The soil properties of these sites (well drained, podzol(ic), sandy, acid soils) are characteristic for the majority of Dutch forests. The fifth forest site (Winterswijk) is located in the eastern part of the Netherlands. This site had periodically high groundwater levels due to the physical characteristics of the boulder clay and the presence of a water-impermeable Lias clay deposit in the subsoil. Within the framework of the Dutch Acidification Programme (Van Breemen & Verstraten

1991), information on vegetation, soil properties and nitrogen cycling had already been collected in these sites (Table 1).

Methods

The leaf litter was sampled by collecting recently fallen leaves from the surface of the forest floor in a dry period at the time of maximum leaf litter production (November). The needle litter was sampled by shaking the trees and collecting the fallen needles. The mesh sizes of the litterbags used in the various experiments (Table 2) was the maximum size possible in order to be able to confine the litter. All litter was air dried before being put into the litterbags. The bags were placed in as many subplots (6—8 m^2) as there were replications (Table 2). Sampling of one litterbag per subplot occurred randomly at various time intervals, ranging from $1\frac{1}{2}$—3 months at the start of the experiment, to 6 months at the end. Most experiments lasted for 3 years. Due to an increased contamination of the bags with mineral soil in some of the sites by soil fauna activity, only the data for the first 2 years are reported in this paper. The content of the sampled litterbags was dried at 70 °C until constant weight was reached in order to determine the remaining mass. After grinding, the total nitrogen concentration in the litter from each litterbag was determined by means of a salicylic acid-thiosulfate modification of the regular Kjehldahl procedure (Bremmer & Mulvaney 1982).

Klason-lignin concentrations in all litter types were determined in a bulk sample of initial (T0) litter. The ethanol-soluble substances were removed by extracting 500 mg ground material with 50 ml 80% ethanol (3 × 30 minutes). The residual solid material was dried overnight at 105 °C and weighed. The residue was treated with 10 ml 72% H_2SO_4 at 30 °C for 1 hour. This mixture was diluted with water to 250 ml and refluxed for 2 hours. The residual solid material was filtered, washed with water, dried overnight at 105 °C and weighed. The amount of lignin was determined as the weight loss upon ignition (650 °C, 2 h) of this residue.

Statistics

Differences between litter type and sampling dates were tested with the non-parametric Mann-Whitney Test (Davis 1986). Differences mentioned in the text are significant at a $P < 0.05$ confidence level, unless a different confidence level is given.

Table 1. Vegetation, soil and nitrogen-cycling characteristics of the studied forests.

	Winterswijk	Buunderkamp	Speuld	Kootwijk	Leuvenum
Tree species	Oak (*Quercus robur*) Beech (*Fagus sylvatica*) Hornbeam (*Carpinus betulum*)	Oak (*Quercus robur*)	Douglas fir (*Pseudotsuga menziesii*)	Douglas fir (*Pseudotsuga menziesii*)	Douglas fir (*Pseudotsuga menziesii*) Scots pine (*Pinus sylvestris*)
Age (years)	55 (Beech) 110 (Oak)	50	30	40	> 100
Soil type *	Dystric Planosol	Fimic Anthrosol	Haplic Podzol	Cambic Podzol	Haplic Arenosol
Ectorganic horizon (LFH)					
Nitrogen (kg N ha^{-1})	1040	1080	850	760	1090
N concentration (%)**	L:1.70 F:2.11 H:1.87	L:2.19 F:2.27	L:1.93 F:2.07	L+F: 1.99	L:1.49 F:1.60 H:1.05
Aboveground litter production (kg N ha^{-1} yr^{-1})					
Total	94	81	40	30	61
Leaves/needles	Oak: 30 Beech: 26	Oak: 58	Douglas fir: 38	Douglas fir: 28	Douglas fir: 38 Scots pine: 8
Nitrogen solute fluxes (kg N ha^{-1} yr^{-1})					
Throughfall	NH_4^+: 34 NO_3^-: 13	NH_4^+: 16 NO_3^-: 6	NH_4^+: 31 NO_3^-: 11	NH_4^+: 30 NO_3^-: 10	NH_4^+: 42 NO_3^-: 13
Leaching	NH_4^+: 1 NO_3^-: 9	NH_4^+: 0 NO_3^-: 7	NH_4^+: 0 NO_3^-: 31	NH_4^+: 0 NO_3^-: 23	NH_4^+: 7 NO_3^-: 17
Nitrogen leached relative to throughfall (%)	96***	32	74	58	44
Nitrogen transformations (kg N ha^{-1} yr^{-1})					
Net mineralization****	LFH: 62 M: 41	LFH: 53 M: 18	LFH: 28 M: 17	LFH: 18 M: 8	LFH: 48 M: 12
Nitrification	LFH: 30 M: 35	LFH: 4 M: 1	LFH: 9 M: 6	LFH: 7 M: 9	LFH 5 M: 1

* According to FAO (1988); ** From Tietema et al. (1992a); *** Including gaseous N loss (35 kg N ha^{-1} yr^{-1}); **** From Tietema et al. (1993); M = top 5 cm of the mineral soil.

Table 2. Specific information on material and methods of the experiments.

Location	litter type (leaves or needles)	mesh size (mm)	initial litter mass (g air-dry)	# of replicates	starting month
Winterswijk	oak	2	7.0	7	Dec 1985
Winterswijk	beech + hornbeam	2	7.0	7	Dec 1985
Buunderkamp	oak	2	6.0	6	Dec 1988
Speuld	Douglas fir	0.6	5.0	5	Dec 1986
Kootwijk	Douglas fir	0.6	5.0	5	Dec 1986
Leuvenum	Douglas fir	0.6	5.0	5	Dec 1989
Leuvenum	scots pine	1	5.0	5	Dec 1989

Results

The initial nitrogen and lignin concentrations in the litter differed between the species (Table 3). The lowest initial nitrogen concentration (1.13%) was measured in the pine needles in Leuvenum. Among the other litter types, initial nitrogen concentrations ranged from 1.53 (Buunderkamp, oak) to 1.82% (Leuvenum, Douglas fir). The highest initial lignin concentrations (41.1, 41.3 and 42.2%) were measured in the Douglas fir needles (Table 3). The mixture of beech and hornbeam leaves in Winterswijk had the lowest lignin concentration (26.8%). Oak leaves contained less lignin in Winterswijk (31.0%) than in Buunderkamp (37.3%).

In all sites, a relatively fast weight loss was measured during the first $1\frac{1}{2}$ months of the decomposition process (Fig. 1). Weight loss during this period ranged from 9% (Speuld, Douglas fir) to 12% (Leuvenum, Douglas fir) of initial weight. In the experiment in Winterswijk, no litterbags were collected after $1\frac{1}{2}$ months. However, the weight loss after 3 months at this site was the highest of all sites for the same incubation time. First-year weight loss ranged from 25.9% (Buunderkamp, oak) to 47.7% (Speuld, Douglas fir) of initial weight.

In general, the data on the remaining amounts of dry weight during the first 24 months fitted significantly to a negative exponential curve:

$$X_{(t)}/X_{(0)} = e^{-kt} \qquad \text{(Wieder \& Lang 1982)}$$

The fast initial weight loss caused in some of the sites a relatively large difference between the measurements of the remaining mass and the regression line after $1\frac{1}{2}$ and 3 months. Introducing an estimate of initial

Table 3. Initial concentrations of nitrogen and lignin, the ratio of the initial nitrogen and lignin concentration, the critical nitrogen concentration and the decomposition constant for the first 24 months of all seven litter types. The linear regression to determine the decomposition constants was carried out for all individual litterbag data and with the use of zero intercept.

Location	litter type leaves or needles	initial nitrogen (%)	initial lignin (%)	lignin/ nitrogen ratio	critical nitrogen (%)	first year weight loss (%)	decomposition constant (k)(yr^{-1})
Winterswijk	oak	1.68	31.0	18.5	2.65	31.4	0.30
Winterswijk	beech + hornbeam	1.73	26.8	15.5	2.65	38.4	0.39
Buunderkamp	oak	1.53	37.3	24.4	2.30	25.9	0.24
Speuld	Douglas fir	1.81	41.3	22.8	2.20	47.7	0.48
Kootwijk	Douglas fir	1.66	42.2	25.4	2.22	37.1	0.37
Leuvenum	Douglas fir	1.82	41.1	22.6	1.90	28.1	0.28
Leuvenum	scots pine	1.13	35.9	31.8	1.68	35.9	0.40

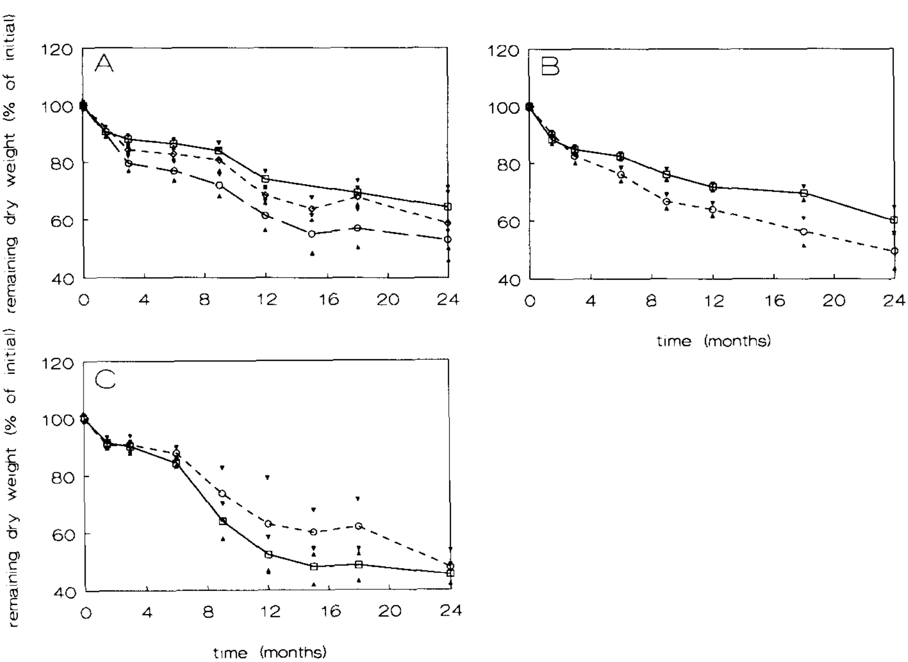

Fig. 1. Remaining dry weight (% of initial amount) as a function of time in decomposing leaves and needles in five forest ecosystems. Fig. A presents data from oak leaves at Buunderkamp (□), from oak leaves (◇) and from a mixture of beech and hornbeam leaves at Winterswijk (O). Fig. B presents data from a mixed coniferous forest ecosystem (Leuvenum). The different lines in Fig. B represent Douglas fir (□) and Scots pine needles (O) at Leuvenum. Fig. C presents data from decomposing Douglas fir needles in two Douglas fir forests. The different lines represent the Speuld site (□) and the Kootwijk site (O). The closed triangular symbols indicate the mean plus (▼) and minus (▲) the standard deviation.

weight loss by leaching (3% of initial weight during the first 1½ months in Buunderkamp, oak leaf litter; unpublished results) in all litters increased the R^2 of the regression and decreased the decomposition constant. However, because the relative order of the decomposition constants between the sites did not change and because many workers use the exponential regression with a fixed (T0) intercept, the reported decomposition constants have been calculated with this latter method. The relative decomposition constants ranged from 0.24 yr^{-1} (Buunderkamp, oak) up to 0.48 yr^{-1} (Speuld, Douglas fir) (Table 3).

The nitrogen concentration in the leaf litter increased during the first 9 or 12 months of the experiment, after which concentration remained at a nearly constant level (Fig. 2A). Only in the Douglas fir needles in Leuvenum was a decrease in nitrogen concentration in the first stage of the decom-

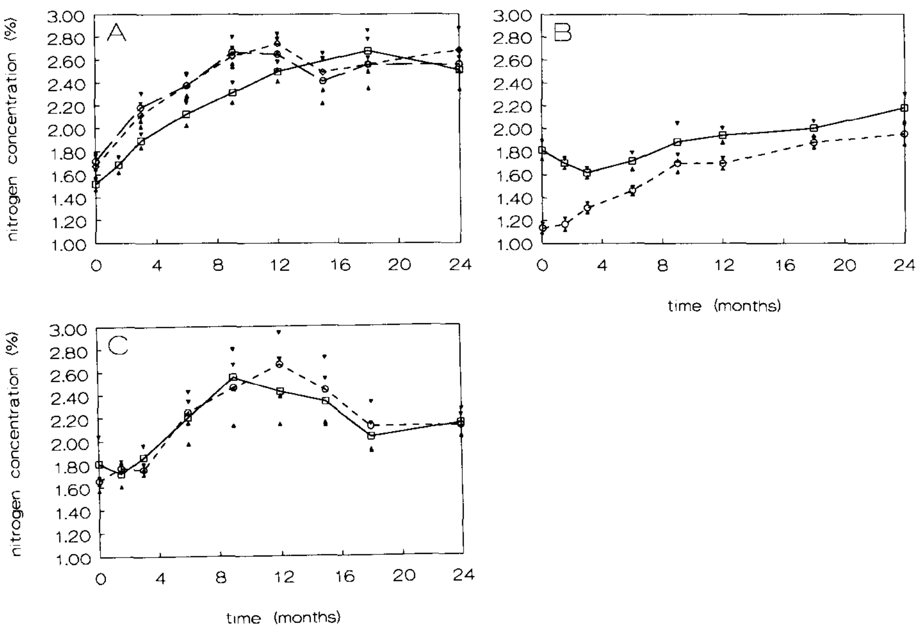

Fig. 2. Nitrogen concentration (% of dry weight) as a function of time in decomposing leaf and needle litter in five forest ecosystems. Fig. A presents data from oak leaves at Buunderkamp (□), from oak leaves (◇) and from a mixture of beech and hornbeam leaves at Winterswijk (O). Fig. B presents data from a mixed coniferous forest ecosystem (Leuvenum). The different lines in Fig. B represent Douglas fir (□) and Scots pine needles (O) at Leuvenum. Fig. C presents data from decomposing Douglas fir needles in two Douglas fir forests. The different lines represent the Speuld site (□) and the Kootwijk site (O). The closed triangular symbols indicate the mean plus (▼) and minus (▲) the standard deviation.

position process found. This decrease was followed by an increase shortly thereafter (Fig. 2B). In the Douglas fir needles in Speuld and Kootwijk, nitrogen concentrations decreased again after the first 12 months (Fig. 2C). In both the Douglas fir needles and in the pine needles in Leuvenum, nitrogen concentration increased during the whole 18-month incubation period (Fig. 2B).

The total amount of nitrogen in the litter decreased (in all needle litter) or remained nearly constant during the first 1½ months of decomposition (Fig. 3). In all litter types except in Leuvenum, the total amount of nitrogen in the litter reached a maximum value after 6 (needles) or 9 months (leaves). This maximum value ranged from 103% (Speuld, Douglas fir) to 128% (Buunderkamp, oak) of the initial amount of nitrogen. After that period the absolute amount of nitrogen decreased. In the deciduous litter this decrease was proportional to weight loss, while in the Douglas fir

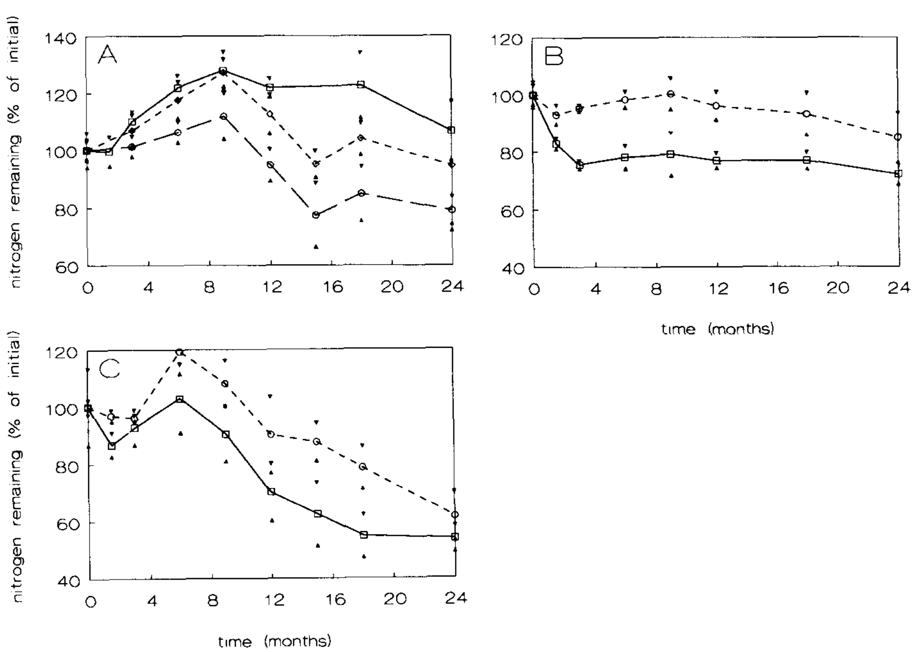

Fig. 3. The total amount of nitrogen (% of initial) as a function of time in decomposing leaf and needle litter in five forest ecosystems. Fig. A presents data from oak leaves at Buunderkamp (□), from oak leaves (◇) and from a mixture of beech and hornbeam leaves at Winterswijk (O). Fig. B presents data from a mixed coniferous forest ecosystem (Leuvenum). The different lines in Fig. B represent Douglas fir (□) and Scots pine needles (O) at Leuvenum. Fig. C represents data from decomposing Douglas fir needles in two Douglas fir forests. The different lines represent Speuld site (□) and the Kootwijk site (O). The closed triangular symbols indicate the mean plus (▼) and minus (▲) the standard deviation.

needles in Speuld and Kootwijk, nitrogen was lost at a higher rate than total weight (Fig. 3C). In the Douglas fir and pine needles in Leuvenum, only a slow and gradual decrease in the amount of nitrogen was measured in the period between 6 and 24 months. The amount of nitrogen in the litter after 24 months equalled 72 and 88% of the initial amount in Douglas fir and Scots pine needles, respectively.

The critical nitrogen concentration (CNC) in all litter types, which is defined as the nitrogen concentration at which nitrogen availability no longer limits microbial activity (Berg & Staaf 1981), can be derived from these data. The CNC equals the nitrogen concentration (Fig. 2) at which the net immobilization phase changes into net mineralization of nitrogen (Fig. 3). The CNC in the deciduous forest litter was lower in the oak leaves in Buunderkamp (2.30%) than in the two litters from Winterswijk

(2.65%) (Table 3). The CNC in the needle litter was found to be lower than in the leaf litter, with the lowest value (1.68%) in the Scots pine needles. Of all the Douglas fir needles, the lowest CNC (1.90%) was found in Leuvenum (Table 3).

Discussion

An analysis of the results obtained from these litterbag experiments, indicates that such an experiment is useful as a way to study decomposition for a limited period of time. After the first 2 years, the results became clouded by increased variation between the replicates which was definitely due to contamination of some of the bags with sand and probably to differences between the replicate bags in the biotic and abiotic environment. The changes in parameters measured, like dry weight and element concentrations, are so small at that stage of decomposition that the variations from naturally occurring processes make the method of limited use. As a consequence, only the first 2 years of decomposition are considered in the analysis of the results.

Variation in climatic conditions between the years may have played a significant role in the decay rate. As influences will be largest during first year decomposition, precipitation and mean temperature data are presented for the first year of all experiments (Table 4). The decomposition constant and the first year weight loss for the oak leaves in Winterswijk (0.30 yr^{-1} and 31.4%) was higher than in Buunderkamp (0.24 yr^{-1} and 25.9%). These differences would probably have been even greater if both experiments would have been carried out in the same year, due to the higher mean temperature in 1989 (Buunderkamp) compared to 1986 (Winterswijk) (Table 4). This difference in mean temperature was mainly

Table 4. Precipitation and temperature data characterizing the environmental conditions of the first year decomposition in the various litterbag experiments. The data (weather station: De Bilt) were taken from the Monthly and Yearly Summary of the Weather in the Netherlands by the Royal Netherlands Meteorological Institute (KNMI).

Sites	First Year	Precipitation (mm)	Mean temperature (°C)
Winterswijk	1986:	715	9.0
Buunderkamp	1989:	661	10.7
Speuld and Kootwijk	1987:	927	8.9
Leuvenum	1990:	716	10.9

caused by a much colder winter in 1986 than in 1989. The annual amount and distribution of precipitation was comparable in both years. Within the Douglas fir needle litters, the Leuvenum site (0.28 yr^{-1} and 28.1%) had a lower decomposition constant and first-year weight loss than both Speuld (0.48 yr^{-1} and 47.7%) and Kootwijk (0.37 yr^{-1} and 37.1%). However, the respective years (Speuld and Kootwijk: 1987 and Leuvenum: 1990) were quite different in amount of precipitation and mean temperature (Table 4). The summer of 1987 was very wet (325 mm precipitation in June, July and August 1987 compared to 156 mm in 1990) which probably explains the relatively large weight loss between 6 and 9 months in Speuld and Kootwijk compared to all other litters. The difference of 2 °C in mean temperature was caused by the cold winter of 1987 compared to 1990. As the relative (contrasting) contribution of both climatic factors are not known, a quantitative analysis of differences in decomposition constants in these litters should be carried out with care.

The decomposition rate of litter and the chemical changes occurring during decomposition are regulated by the interaction between litter quality, soil organisms and environmental conditions (Berg & Staaf 1981; McClaugherty & Berg 1987). Different indices of litter quality are considered to be important in regulating the decay rate, such as the initial nitrogen concentration (Melin 1930), the initial lignin concentration (Fogel & Cromack 1977) and the initial lignin-to-nitrogen ratio (Melillo et al. 1982). Despite the differences in atmospheric nitrogen input to these sites (Table 1), no significant correlation was found between these litter quality indices and the decomposition rate constant (k), nor with the first-year weight loss. A significant linear relationship was found between the initial lignin-to-nitrogen ratio and critical nitrogen concentration (CNC) (Fig. 4). The CNC is determined by the microbial C-to-N ratio and by the efficiency of substrate utilization by microbes (Parnas 1975). The relationship between lignin-to-nitrogen ratio and CNC suggest an effect of initial litter quality on nitrogen dynamics in decaying litter in these forest soils.

The two deciduous forests clearly differed in nitrogen status. The oak forest of Buunderkamp can be described as a system in which nitrogen is relatively limited. The site has low atmospheric nitrogen input, low nitrification rate, low inorganic nitrogen concentrations in soil water (Tietema et al. 1993) and low NO_3^- leaching (Table 1). The oak-beech forest of Winterswijk had relatively high nitrogen inputs, high nitrification rates, high inorganic nitrogen concentrations (mainly NO_3^-; Tietema & Verstraten 1991), relatively low NO_3^- leaching losses, but quantitatively significant gaseous nitrogen losses by denitrification (Tietema et al. 1991). The large difference in nitrogen status is illustrated by the percentage of (throughfall) input leaving the soil. In Buunderkamp, the total nitrogen output

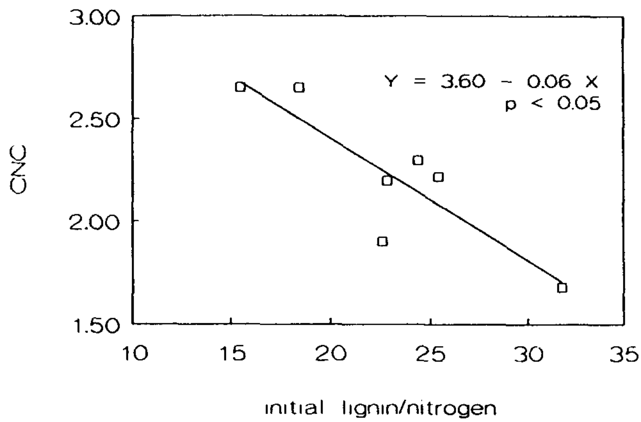

Fig. 4. Relation between initial lignin-to-nitrogen ratio and critical nitrogen concentration (CNC) in seven forest litters.

amounted to 32% of nitrogen input by throughfall, while in Winterswijk nearly 96% of the input left the forest.

By assuming that these two sites are representative of a transect ranging from a nitrogen-limited to a nitrogen-saturated situation, it is possible to speculate about the change in decomposition and nitrogen dynamics in decaying litter as a result of increased nitrogen availability. The oak leaf litter of Winterswijk, compared to that of Buunderkamp, had a higher initial nitrogen concentration (1.68% vs. 1.53%), a lower initial lignin concentration (31.0% vs. 37.3%), a higher critical nitrogen concentration (2.65% vs. 2.30%) and a higher decomposition rate (0.30 yr^{-1} vs. 0.24 yr^{-1}). The higher nitrogen and lower initial lignin concentration resulted in a lower initial lignin-to-nitrogen ratio (18.5 vs. 24.4). This comparison indicated a higher initial litter quality in Winterswijk than in Buunderkamp and a subsequent higher decomposition rate. These observations are in agreement with the findings of McNulty et al. (1991). They found a strong negative correlation between nitrogen deposition rate and lignin-to-nitrogen ratio in the foliage of a large number of spruce-fir forests in the USA, which also suggest higher decomposition rates with increased litter quality as a result of increased atmospheric nitrogen input.

Fog (1988) concluded from an extensive literature survey that in many cases nitrogen additions produced no effect, or sometimes even a negative effect on decomposition rate. From these observations it can be hypothesized that increased nitrogen availability as such will not cause higher decomposition rates directly, but it will stimulate decomposition over the long term via increased litter quality. The obvious link between litter quality and decomposition rate, however, should be questioned following the observations of Berg & Ekbohm (1991). They measured in nutrient-rich litters a lower accumulated weight loss after 3—4 years, whereas they had initially higher weight loss rates during the first 12—18 months.

The nitrogen limitation and saturation characteristics in both sites can partly be attributed to differences in nitrogen storage during the first year of decomposition. This is indicated by the annual budget of mineral nitrogen within the first year litter. The budget was calculated by relating first year nitrogen dynamics in newly produced litter with the annual atmospheric (throughfall) nitrogen deposition (Table 5). During the first year of litter decomposition, 55% of total atmospheric nitrogen input (NH_4^+ + NO_3^-) was immobilized in the oak leaves in Buunderkamp. In the Winterswijk leaf litter this value amounted to only 2%. The impact of this 55% immobilization of the atmospheric deposition is enormous, considering the fact that each year more fresh litter is produced, again immobilizing that percentage of atmospheric input. On an annual basis this would mean that only 45% of the throughfall mineral nitrogen input (10 kg N ha^{-1}) would reach the (mineralizing) older litter layers in Buunderkamp, in contrast with 94% (44 kg N ha^{-1}) in Winterswijk. This difference in first-year net nitrogen immobilization between the two sites was caused by the fact that nitrogen concentration in the oak leaves in Buunderkamp was still increasing at the beginning of the mineralization phase, while in Winterswijk, in the oak as well as in the beech and hornbeam leaves, the

Table 5. Nitrogen budget of first year leaf and needle litter decomposition.

Location	litter type leaves or needles	annual leaf or needle litterfall	storage in litter after 12 months	immobilized in 12 months	relative to input per site
			kg N ha^{-1} yr^{-1}		%
Winterswijk	oak	30	34	+4	6
Winterswijk	beech + hornbeam	26	25	−1	
Buunderkamp	oak	58	70	+12	55
Speuld	Douglas fir	26	18	−8	20
Kootwijk	Douglas fir	17	15	−2	5
Leuvenum	Douglas fir	38	29	−9	
Leuvenum	scots pine	8	7	−1	18

nitrogen concentration remained at a nearly constant level during the mineralization phase (Fig. 2). An increasing nitrogen concentration during the mineralization phase signifies a relatively slow release of nitrogen compared to carbon, which can be attributed to a relatively large part of the nitrogen being bound in slowly decomposing compounds or to an immobilization of mineralized nitrogen into stable organic compounds. In contrast, a constant nitrogen concentration during the mineralization phase, as was found in Winterswijk, marks a relatively equal partitioning of nitrogen in slowly and fast decomposing compounds. This observation underlines the relation between initial litter quality and nitrogen dynamics during the first stage of the decomposition process as was described earlier.

The differences in nitrogen status between the three coniferous forest sites are less profound. The two Douglas fir locations, Speuld and Kootwijk, resemble each other very closely in nitrogen cycling (Table 1). The mixed stand of Leuvenum, however, showed some differences compared to Speuld and Kootwijk. The Leuvenum site had a higher atmospheric nitrogen input, a much lower nitrification rate and much lower total nitrogen concentrations in the ectorganic (LFH) layer (Table 1). In comparison with Speuld and Kootwijk, where 74% and 58% respectively of nitrogen input was leached out of the system, in Leuvenum only 44% of input was lost. Differences in decomposition characteristics between the Douglas fir litter in Leuvenum and in the other coniferous forests were found as well. Despite nearly equal initial substrate quality measures (initial nitrogen and lignin concentration and lignin-to-nitrogen ratio (Table 2)), completely different nitrogen dynamics was found in the Douglas fir litter in Leuvenum compared to the other Douglas fir forests. The nitrogen concentration in the Douglas fir needle litter increased at a much slower rate in Leuvenum than in Speuld and Leuvenum (Fig. 2). The decomposition constant in Leuvenum was found to be lower (0.28 yr^{-1}) than in Speuld (0.48 yr^{-1}) and Kootwijk (0.37 yr^{-1}), which, however, was probably partly caused by differences in climatic conditions in the first years of both experiments. The amount of nitrogen in the Douglas fir litter in Speuld and Kootwijk showed a relatively fast net immobilization of nitrogen, followed by a fast mineralization. In Leuvenum, the changes in the total amount of nitrogen were very small during the first two years of decomposition.

Differences are also seen in the relation between weight loss and nitrogen concentration in the decaying litter (Fig. 5). In all litters, a linear relation was found between these two parameters as long as there was a net immobilization of nitrogen in the litter. After that immobilization phase, nitrogen concentrations remained constant or even decreased in

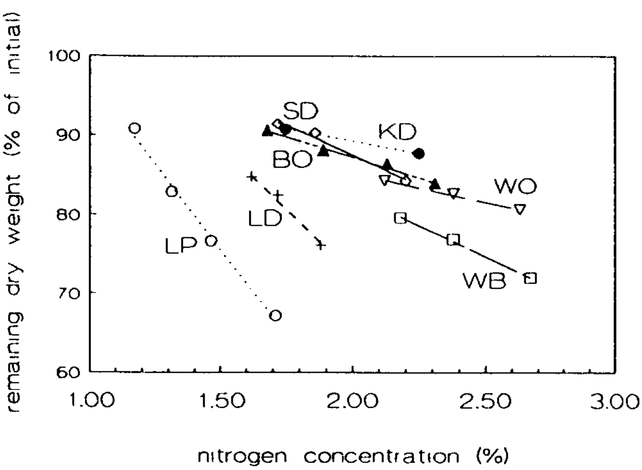

Fig. 5. Relation between nitrogen concentration (%) and remaining weight of oak leaf litter of Winterswijk (WO) and Buunderkamp (BO), beech and hornbeam leaf litter in Winterswijk (WB), Scots pine needle litter in Leuvenum (LP) and Douglas fir needle litter in Leuvenum (LD), Speuld (SD) and Kootwijk (KD). Only data points within the 'immobilization phase' were used in this regression. Coefficients of determination (r^2), intercepts and slopes of the linear relationships are summarized in Table 6.

some litter types, which would change this relation. The slope of the regression line represents the amount of carbon respired per net unit of nitrogen immobilized (Aber & Melillo 1980), which can be considered to be a measured of the efficiency of substrate utilization for assimilation of microbial biomass and/or of secondary compounds. The steeper (more negative) the slope, the larger the amount of C needed to be respired for the net immobilization of one unit of nitrogen. In the Douglas fir litter in Leuvenum, a much higher value for the slope (−32.8) was found than in Speuld (−15.0) and Kootwijk (−6.0) (Table 6), which would signify a much lower efficiency of substrate utilization. The differences in nitrogen dynamics in Douglas fir needle litter during the first 2 years of decomposition between Leuvenum and Speuld are underlined by comparative studies of nitrogen cycling and microbial activity in the whole ectorganic (LFH) layer. Tietema & Wessel (1992) measured lower gross nitrogen transformation rates and thus a lower nitrogen turnover rate in Leuvenum, and Tietema et al. (1992b) found a lower respiration rate in Leuvenum compared to Speuld. The different nitrogen dynamics in the Douglas fir needle litter must be due to site specific environmental factors as the needle litters have a comparable quality. A possible explanation could be that the microbial community in the forest floor in Leuvenum is adapted

Table 6. Slopes, intercepts, coefficients of determination (r^2) and number of data points (n) used for the relationships between nitrogen concentration and remaining weight of litter in the 'immolibization phase'.

Location	litter type leaves or needles	slope	intercept	r^2	n
Winterswijk	oak	−7.1	99.5	0.997	3
Winterswijk	beech + hornbeam	−15.7	114.0	0.998	3
Buunderkamp	oak	−10.0	107.2	0.987	4
Speuld	Douglas fir	−15.0	117.4	0.984	3
Kootwijk	Douglas fir	−6.0	101.3	*	2
Leuvenum	Douglas fir	−32.8	138.1	0.985	3
Leuvenum	scots pine	−43.8	140.6	0.978	4

* Due to the availability of only two data points, no statistics could be computed for the Douglas fir litter of Kootwijk.

to the low quality pine needles. This is underlined by the even steeper slope (−43.8) and thus a lower substrate utilization efficiency in pine needles. An alternative explanation might be that microbial metabolites released during decomposition of the pine needles interfere with nitrogen dynamics in decaying Douglas fir needles.

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