

ORIGINAL PAPER

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Nitrogen supply effects on productivity and potential leaf litter decay of *Carex* species from peatlands differing in nutrient limitation

Received: 22 April 1995 / Accepted: 19 June 1995

Abstract We investigated the effect of increased N-supply on productivity and potential litter decay rates of *Carex* species, which are the dominant vascular plant species in peatlands in the Netherlands. We hypothesized that: (1) under conditions of N-limited plant growth, increased N-supply will lead to increased productivity but will not affect C:N ratios of plant litter and potential decay rates of that litter; and (2) under conditions of P-limited plant growth, increased N-supply will not affect productivity but it will lead to lower C:N ratios in plant litter and thereby to a higher potential decay rate of that litter. These hypotheses were tested by fertilization experiments (addition of $10 \text{ g N m}^{-2} \text{ year}^{-1}$) in peatlands in which plant growth was N-limited and P-limited, respectively. We investigated the effects of fertilization on net C-fixation by plant biomass, N uptake, leaf litter chemistry and potential leaf litter decay. In a P-limited peatland, dominated by *Carex lasiocarpa*, there was no significant increase of net C-fixation by plant biomass upon enhanced N-supply, although N-uptake had increased significantly compared with the unfertilized control. Due to the N-fertilization the C:N ratio in the plant biomass decreased significantly. Similarly, the C:N ratio of leaf litter produced at the end of the experiment showed a significant decrease upon enhanced N-supply. The potential decay rate of that litter, measured as CO_2 -evolution from the litter under aerobic conditions, was significantly increased upon enhanced N-supply. In a N-limited peatland, dominated by *C. acutiformis*, the net C-fixation by plant biomass increased with increasing N-supply, whereas the increase in N-uptake was not significant. The C:N ratio of both living plant material and of dead leaves did not

change in response to N-fertilization. The potential decay rate of the leaf litter was not affected by N-supply. The results agree with our hypotheses. This implies that atmospheric N-deposition may affect the CO_2 -sink function of peatlands, but the effect is dependent on the nature of nutrient limitation. In peatlands where plant growth is N-limited, increased N-supply leads to an increase in the net accumulation of C. Under conditions of P-limited plant growth, however, the net C-accumulation will decrease, because productivity is not further increased, whereas the amount of C lost through decomposition of dead organic matter is increased. As plant growth in most terrestrial ecosystems is N-limited, increased N-supply will in most peatlands lead to an increase of net C-accumulation.

Key words CO_2 -sink · Decomposition · Global change · Nitrogen deposition · Nutrient limitation

Introduction

The rate of organic matter accumulation in peatlands is determined by the balance between the amount of C fixed in primary production and the amount of C lost due to decomposition of dead organic matter. The net rate of C accumulation in peatlands is mainly determined by low decomposition rates of dead organic material and not by high rates of primary production (Clymo 1984; Malmer and Wallén 1993). Due to the relatively large peat cover on earth (Clymo 1984), changes in the CO_2 -sink function of peatlands will affect the global C budget (Billings 1987; Gorham 1991; Chapin et al. 1992; Woodwell 1994). Therefore, environmental changes which affect this CO_2 -sink function might be important contributors to global change. Nowadays, much research effort is spent on the effects of global warming on the CO_2 -sink function of (sub-)Arctic peatlands (e.g. Chapin et al. 1992; Shaver et al. 1992; Melillo et al. 1993; Oechel et al. 1993). One

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of the major conclusions is that if global warming leads to higher release rates of nutrients from soil organic matter in these peatlands, there will be profound effects on the C balance of these peatlands (Shaver et al. 1992). However, there is no conclusive evidence that at the predicted levels of global warming nutrient release from (sub-)Arctic soils will indeed increase (Jonasson et al. 1993).

A point which has received relatively little attention is how changes in external nutrient inputs might affect the C balance of peatlands. For terrestrial ecosystems it has been established that primary production is very often limited by N availability (e.g., Tilman 1984; Vermeer 1986a, b; Bobbink et al. 1988; Aerts 1989; Aerts and De Caluwe 1989; Vitousek and Howarth 1991). Similarly, decomposition of dead organic matter is, in many cases, determined by the N concentration or the C:N ratio in the dead organic matter (Witkamp 1966; Berg and Staaf 1980; Taylor et al. 1989; Tian et al. 1992). Therefore, changes in atmospheric N deposition may affect the C balance of peatlands, due to effects on both productivity and decomposition.

Aerts et al. (1992a) postulated the following hypothetical scheme for the effects of atmospheric N-deposition on the C balance of peatlands: increased atmospheric N-deposition initially leads to increased productivity and thereby to an increased rate of net C accumulation in peatlands. In the long-term, however, plant growth will become P-limited instead of N-limited, so no further increase in the net C-fixation rate by plant biomass will occur. However, due to the change from N-limited growth to P-limited growth the N-concentrations in living plant parts and in plant litter will increase. As a result of the increased N-concentration in plant litter, the decomposition rate of this dead plant material will increase. Thus, a high rate of N-deposition may in the long-term reduce the CO₂-sink function of peatlands, because it does not increase productivity further, but it increases decomposition rates. There is increasing evidence that increased N-deposition indeed leads to a shift from N-limited plant growth to P-limited plant growth in regions with high atmospheric N-deposition, such as the Netherlands and southern Sweden (Tamm 1954; Vermeer 1986a,b; Aerts and Berendse 1988; Malmer 1990; Verhoeven and Schmitz 1991; Aerts et al. 1992a). However, there is only very limited evidence for the postulated effect of increased N-supply on litter N-concentrations and litter decay rates. The most clear-cut results were obtained by Coulson and Butterfield (1978), who found that litter N-concentrations in vascular plant species from blanket bogs increased after N-fertilization and that this in turn resulted in higher decomposition rates. Pastor et al. (1987), however, found that annual decay rates of litter of *Schizachyrium scoparium* were highly correlated with the N content of the litter but not with fertilizer additions. This lack of correlation with fertilizer additions was due to the fact that litter N-con-

centrations were not, or only weakly, correlated with fertilizer addition.

The aim of the present study was to investigate the effect of increased atmospheric N-deposition on productivity and potential decay rates of *Carex* species growing in peatlands in the Netherlands. Although C losses due to root exudation might be important in the C balance of peatlands we did not investigate this process in our experiments. Atmospheric N-deposition in north-west Europe has doubled from 1950 until 1980 and the highest values are nowadays recorded in the Netherlands (Asman et al. 1988). For low vegetation in the Netherlands N-deposition amounts to about 3–4 g N m⁻² year⁻¹ (Bobbink and Heil 1993). Apart from this direct effect on N-availability, an indirect effect is realized through an increase in productivity, litter production, organic matter accumulation, and N-mineralization (Aerts 1993). As a result, total N-availability for plant growth has in the long term increased to maximum values of 17 g N m⁻² year⁻¹ in Dutch heathlands (Berendse 1990) and to about 24 g N m⁻² year⁻¹ in Dutch peatlands dominated by *Carex acutiformis* (Verhoeven et al. 1990). These high levels of N-availability have profound effects on nutrient cycling and species composition in many Dutch ecosystems (Hey and Schneider 1991). We hypothesized that: (1) under conditions of N-limited plant growth, increased N-deposition will lead to increased productivity, but will not affect C:N ratios of plant litter and potential decay rates of that litter; and (2) under conditions of P-limited plant growth, increased N-deposition will not affect productivity, but it will lead to lower C:N ratios in plant litter and thereby to a higher potential decay rate of that litter. These hypotheses were tested by means of fertilization experiments in a N-limited and a P-limited peatland, respectively. We investigated the effects of N-fertilization on growth responses of the dominant *Carex* species, leaf litter chemistry, and on potential leaf litter decay rates.

Material and methods

Study sites

The field experiments were conducted in 1992 at two peatlands dominated (> 70% of total above-ground vascular plant biomass) by *Carex acutiformis* and *C. lasiocarpa*, respectively. A detailed description of these study sites, which are located about 10 km north of the city of Utrecht (The Netherlands), is given by Verhoeven and Arts (1987) and Verhoeven and Schmitz (1991). According to vegetational and hydrological criteria the *C. lasiocarpa* peatland can be classified as a low-productivity mesotrophic fen and the *Carex acutiformis* peatland as a high-productivity eutrophic fen (Björk 1967; Kvet and Husák 1978; Ruuhijärvi 1983; Verhoeven et al. 1988). Maximum above-ground biomass in the *C. lasiocarpa* peatland is about 300 g/m² and in the *C. acutiformis* peatland it is about 800 g/m² (Verhoeven et al. 1983). To prevent succession of these peatlands to alder woodland both sites are annually mown in summer and the mown biomass is removed. Due to the removal of biomass and nutrients there are profound effects on nutrient cycling at these sites. Fertilization experiments (Verhoeven and Schmitz

1991) and ecosystem nutrient budgets (Koerselman and Verhoeven 1992) have shown that the overall effect of the mowing regime is that plant growth in the *C. lasiocarpa* peatland is P-limited, whereas plant growth in the *C. acutiformis* peatland is N-limited.

Growth experiments

In early spring (March 1992) tillers of both species were collected at their growing sites and the dead plant parts were removed. The tillers were gently separated into individual plants. Shoots and roots of both species were cut back to a length of 4 cm and 10 cm, respectively. To promote growth, the plants were pre-grown for 1 month in a greenhouse (15 °C) in pots filled with sand. Nutrients were supplied once a week and each plant received 10 ml of a low-strength nutrient solution. The composition of this solution was: 0.47 mM NH_4Cl , 0.19 mM H_2PO_4^- , 0.98 mM K^+ , 0.27 mM Mg^{2+} , 2 μM Mn^{2+} , 0.85 mM Zn^{2+} , 0.15 μM Cu^{2+} , 20 μM H_3BO_3 , 0.25 mM MoO_4^- and 40 μM Fe-EDTA.

In April 1992, 15 plants of each species were randomly taken from the plants in the greenhouse and the ratio between fresh weight and dry weight was determined after drying the plants for 48 h at 70 °C. These plants were further analysed for their C, N, and P contents (see 'Nutrient analyses'). In this way we were able to estimate the relationship between initial fresh weight, initial dry weight and initial C, N and P contents of the plants. This relation was further used to calculate these parameters for the plants which were used for the experiments.

Next, 36 plants of *C. lasiocarpa* and of *C. acutiformis* were randomly chosen from the plants which had been grown in the greenhouse. The fresh weight of each plant was determined, and from this we estimated the initial dry weight and the initial C, N and P content of each individual plant. These plants were transferred to their native growing site and each individual plant was placed in a polyvinyl chloride (PVC) tube filled with soil material of the peatland. The tubes had open ends on both sides. They were 50 cm long and had a diameter of 4.6 cm. In the tubes 10 holes (1.0 cm diameter) were present to allow free access of soil water. The tubes were placed in the soil so that the soil level inside the tubes was equal to the soil level outside the tubes.

In both peatlands there were two fertilizer treatments: an unfertilized control (0N) and a treatment which received 10 g N $\text{m}^{-2}\text{year}^{-1}$ (10N). For each treatment there were 18 replicate plants. In both peatlands N was supplied as NH_4Cl , dissolved in 25 ml of distilled water. This solution was added every 2–3 weeks during the growing season.

At the end of the growing season (September 1992) nine replicate plants of each treatment and each species were harvested by taking the tubes out of the soil. In the laboratory the soil was washed out of the root system. The plants were dried (70 °C, 48 h) and the dry mass was determined. In each plant the C, N and P concentration was determined (see 'Nutrient analyses'). As we had estimates of the initial dry weight and nutrient concentrations of each individual plant, we were able to calculate the net C-fixation and the net nutrient uptake of each individual plant.

Decomposition experiments

The remaining plants (nine replicates for each combination of species and fertilizer level) were left in the field until leaf senescence started (November 1992). Senesced leaf material was removed every week from each plant and the material was bulked for each individual plant. In both species, leaf mass contributes about 45% to total plant mass (Aerts et al. 1992b). Decay potential of the leaf litter was determined by measuring CO_2 -evolution rates on this material (cf. Taylor and Parkinson 1988a; Hogg 1993). To this end, 0.500 g (*C. acutiformis*) or 0.100 g (*C. lasiocarpa*) of air-dried litter of each species and each treatment was incubated by re-wetting the

material until saturation with a mixture of mire water from each site. Incubation was performed in 100-ml glass incubation jars. The bottom of each jar was covered with glass marbles and 5-ml potassium sulphate. The potassium sulphate was added to keep the relative humidity in the jars during incubation at a constant level of 97% at 20 °C (Fritschen and Lloyd 1979). In this way, drying-out of the litter was prevented. The litter was placed on gauze on top of the marbles in such a way that there was no contact between the potassium sulphate and the litter. All the incubation jars were kept in a climate room at 20 °C and with a constant relative humidity of 97%. As we were not interested in the strong initial respiration flushes after incubation of the litter (cf. Taylor and Parkinson 1988b) microbial respiration was measured 7 days after incubation of the litter. For the measurements, the glass jars were closed for a period of 4 h (*C. acutiformis*) or 17 h (*C. lasiocarpa*) and at the start and end of this period 5-ml gas samples were taken from the jars and analysed for CO_2 on a gas chromatograph (Hewlett Packard 5890A, Hewlett Packard, Pennsylvania, USA) equipped with a thermal conductivity detector. The calculated CO_2 -fluxes were corrected for the amount of CO_2 dissolved in the potassium sulphate solution. Pilot studies showed that CO_2 -fluxes were linearly proportional to incubation time up to a period of 24 h. After the measurements the litter was dried (48 h, 70 °C) and analysed (see 'Nutrient analyses'). The CO_2 -evolution rate was calculated per unit litter dry mass per hour.

Nutrient analyses

Total C and N content of leaf litter was determined by dry combustion of 2.000 mg ground plant material with an elemental analyser (Carlo Erba model 1106, Carlo Erba, Milano, Italy).

Total N and P content was determined by acid digestion according to a salicylic acid thiosulphate modification of the Kjeldahl method (Page et al. 1982). For this purpose, 150 mg ground plant material was digested in 5-ml 30 N sulphuric acid and a mixture of sodium sulphate, copper sulphate and selenium. The diluted digestions were analysed colorimetrically on a continuous flow analyser (Skalar SA-40, Skalar, Breda, The Netherlands) using the indophenolblue method with salicylate for ammonium (Bietz 1974) and the ammonium molybdate method for phosphorus (Lennox 1979). Nitrogen concentrations determined with the elemental analyser were in general 10% higher than the values determined with the Kjeldahl method. For all calculations we used the N-concentrations determined with the elemental analyser.

Statistical analysis

Data were statistically analysed using the SAS statistical package (SAS Institute Inc. 1985). Pairwise comparisons between parameters of unfertilized and fertilized plants were made using Student's *t*-test.

CO_2 evolution rates were linearly regressed against litter quality parameters. The significance of the regression coefficients were determined by Student's *t*-test.

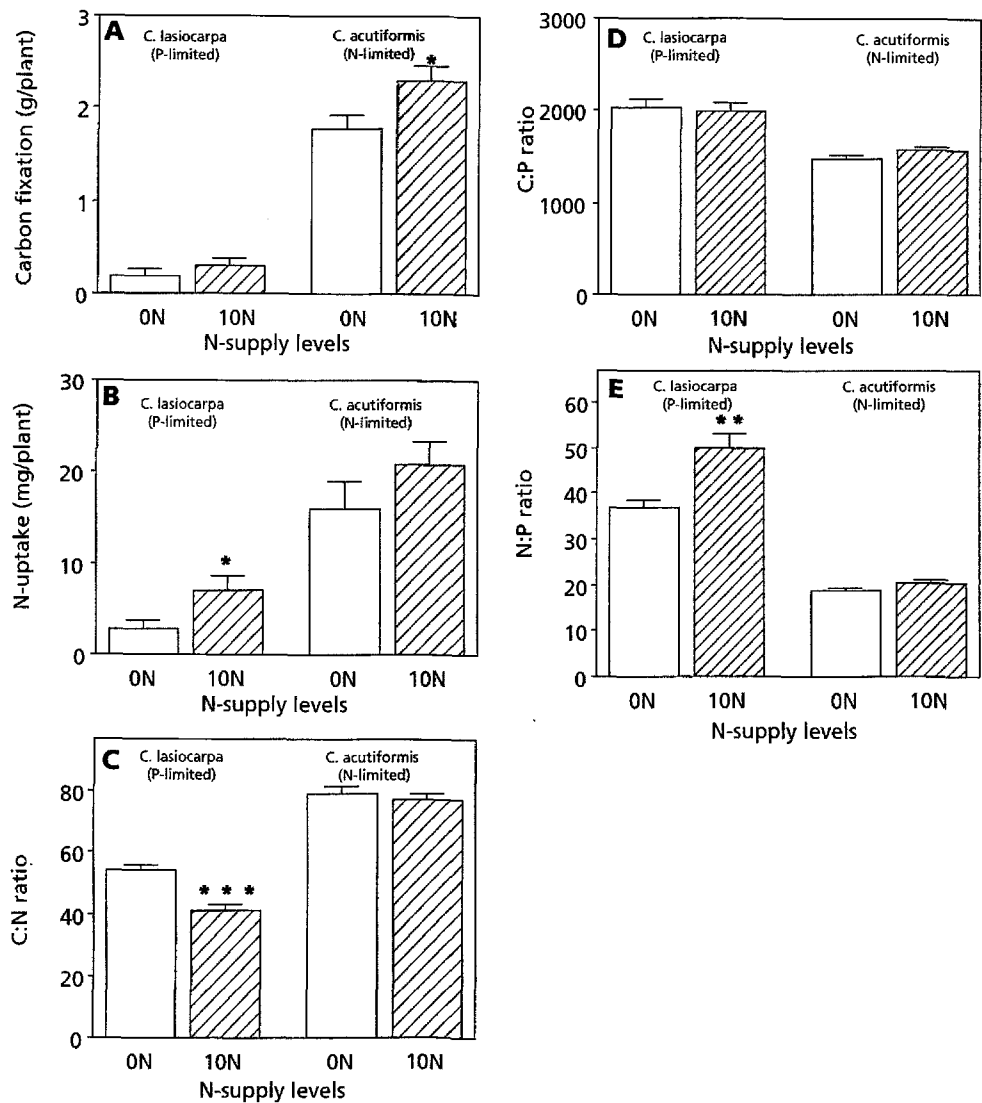
Results

Growth experiments

P-limited peatland

In the peatland dominated by *C. lasiocarpa* there was no significant increase of the net C-fixation upon enhanced N supply (Fig. 1A), although N-uptake had

Fig. 1 A Net carbon fixation, B N-uptake, C C:N ratio, D C:P ratio and E N:P ratio of plants of *Carex lasiocarpa* and *C. acutiformis* when grown at different levels of N-supply. Error bars are SE ($n = 9$). Treatments: unfertilized control (0N); 10 g N m⁻² year⁻¹ (10N). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$



increased significantly compared with the unfertilized control (Fig. 1B). Due to the N-fertilization the C:N ratio in the plant biomass decreased significantly (Fig. 1C), whereas the C:P ratio in the plants was not affected by increased N-supply (Fig. 1D). The N:P ratio showed a significant increase after N-fertilization (Fig. 1E).

N-limited peatland

In the N-limited peatland there was a significant increase of the net C-fixation in the fertilized treatment (Fig. 1A). Compared with the P-limited peatland the amount of C fixed was much higher ($P < 0.0001$), thereby reflecting the more productive growing conditions at the N-limited site. The increase in N-uptake in the fertilized treatment was not significant (Fig. 1B). Similarly, the C:N ratio, the C:P ratio and the N:P ratio of the living biomass were not significantly affected by N-fertilization (Fig. 1C–E).

Decomposition experiments

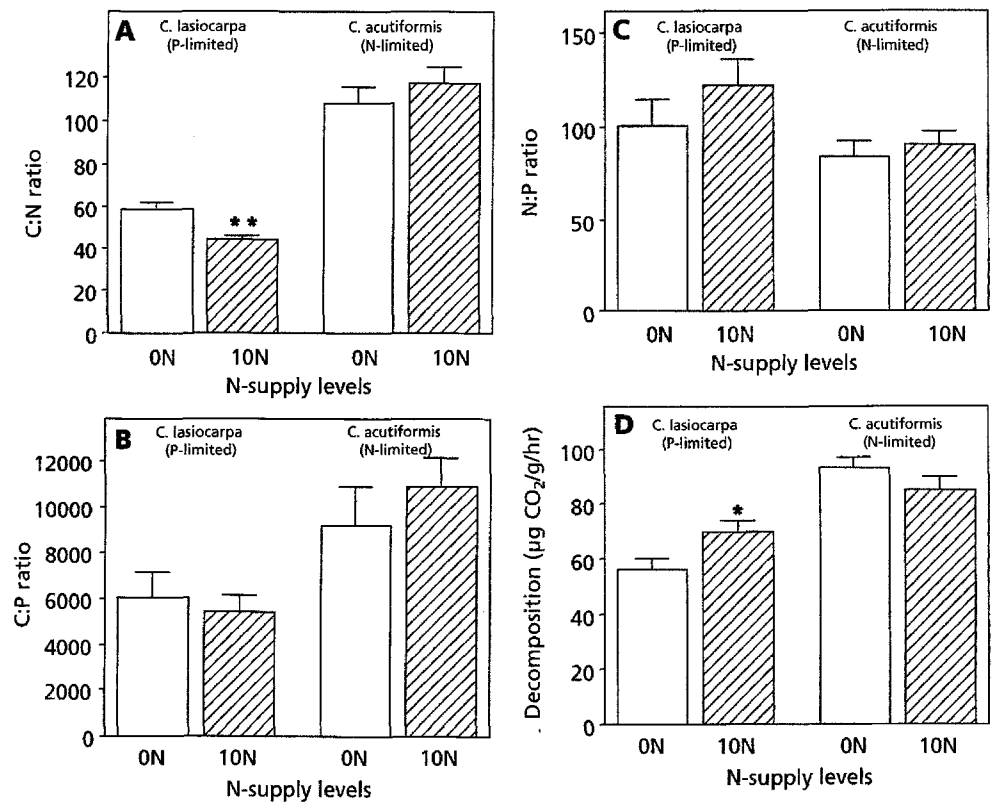
P-limited peatland

In the peatland dominated by *C. lasiocarpa* the C:N ratio of leaf litter showed a significant decrease after N-fertilization (Fig. 2A). However, there was no effect

Table 1 Results of linear regressions of CO₂-evolution rates (mg CO₂ g⁻¹ h⁻¹) measured after 7 days of incubation of *Carex* leaf litters against litter quality parameters

Regression	r ²	Significance
<i>Carex lasiocarpa</i> (P-limited) (df = 12)		
CO ₂ = 0.098 - 0.00064 C:N	0.30	P < 0.05
CO ₂ = 0.075 - 0.09546 C:P	0.10	NS
CO ₂ = 0.062 + 0.00004 N:P	0.01	NS
<i>Carex acutiformis</i> (N-limited) (df = 16)		
CO ₂ = 0.118 - 0.00026 C:N	0.23	P < 0.05
CO ₂ = 0.107 - 0.00001 C:P	0.36	P < 0.01
CO ₂ = 0.110 - 0.06970 N:P	0.23	P < 0.05

Fig. 2 A C:N ratio, B C:P ratio, C N:P ratio and D CO₂-evolution of leaf litter of *Carex lasiocarpa* and *C. acutiformis* plants grown at different levels of N-supply. Error bars are SD (*C. lasiocarpa*: unfertilized $n = 6$; N-fertilized $n = 8$; *C. acutiformis* $n = 9$). Treatments: unfertilized control (0N); 10 g N m⁻² year⁻¹ (10N). * $P < 0.05$; ** $P < 0.0001$



of N-fertilization on the C:P and the N:P ratio in the leaf litter (Fig. 2B–C). The potential decay rate, measured as CO₂-evolution from the litter under standard laboratory conditions, was significantly increased upon enhanced N-supply (Fig. 2D). Linear regression analysis showed that the CO₂-evolution rate was negatively related with the C:N ratio of the litter (Table 1). However, the r^2 value was relatively low, thus the C:N ratio of the litter explained only a relatively low percentage of the variance in CO₂-evolution rates. There were no significant relations of CO₂-evolution with the C:P ratio or the N:P ratio of the litter.

N-limited peatland

The C:N ratio of leaf litter of *C. acutiformis* was not significantly affected by N-fertilization (Fig. 2A). The same holds for the C:P ratio and the N:P ratio of the leaf litter (Fig. 2B–C). The potential decay rate, measured as the CO₂-evolution of leaf litter under standard laboratory conditions, was also not affected by N-supply (Fig. 2D). Although there were no treatment effects on litter quality parameters and on CO₂-evolution rates, there were significant negative relations between the CO₂-evolution rate from leaf litter of *C. acutiformis* and the C:N ratio, the C:P ratio and the N:P ratio of that litter (Table 1). However, for all these litter quality parameters the r^2 values were relatively low. In other words, they explained only a relatively low percentage of the variance in CO₂-evolution rates.

Discussion

We conducted our study in peatlands from the temperate zone which differed in nutrient limitation. In the P-limited peatland, *C. lasiocarpa* comprised about 70% of total above-ground vascular plant biomass. In the N-limited peatland, *C. acutiformis* comprised about 85% of total above-ground vascular plant biomass. Thus, the results obtained with these species reflect to a large extent the response of vascular plants in these peatlands. Our study is in fact mirroring many global change studies in which effects of rising CO₂-concentrations in the atmosphere on ecosystem functioning are investigated (e.g. Chapin et al. 1992; Shaver et al. 1992; Melillo et al. 1993). We, on the other hand, investigated the effect of increased levels of N supply on the CO₂-sink function of peatlands and thus on the exchange of CO₂ between peatlands and the atmosphere. Due to the relatively large peat cover on earth (Clymo 1984), changes in the CO₂-sink function of peatlands will affect the global C budget (Chapin et al. 1992; Gorham 1994; Wieder and Yavitt 1994; Woodwell 1994). Our results show that under conditions of N-limited plant growth, productivity in the peatland under study was positively affected by enhanced N-supply, whereas litter chemistry and the decay rate of plant litter were not affected. This implies that under conditions of N-limited plant growth the CO₂-sink function of peatlands is increased in response to increased levels of atmospheric N-deposition. Under

conditions of P-limited plant growth in peatlands, however, an increased level of N-supply had no effect on plant productivity, whereas it led to lower C:N ratios in plant litter and thereby to a higher potential decay rate of that litter. Thus, under conditions of P-limited plant growth, the CO₂-sink function of peatlands may decrease upon enhanced N-supply. Thus, the effects of atmospheric N-deposition on the CO₂-sink function of peatlands depend on the type of nutrient limitation for plant growth in these peatlands. As N-limited plant growth is prevailing in most terrestrial ecosystems (Vitousek and Howarth 1991), it is to be expected that increases of atmospheric N-deposition will, in general, lead to increased C-accumulation in most peatlands. However, in regions where levels of atmospheric N-deposition are already high (north-west Europe) P-limited plant growth may occur (see e.g. Tamm 1954; Vermeer 1986a, b; Aerts and Berendse 1988; Malmer 1990; Verhoeven and Schmitz 1991; Aerts et al. 1992a), and in these cases increased N-deposition may lead to a reduction of the CO₂-sink function of peatlands. As this study provides only qualitative indications of the direction of change of productivity and decomposition, there is clearly a need for more quantitative data at the ecosystem level on the effects of atmospheric N-deposition on the role of peatlands in the global C budget.

Three points should be emphasized with regards to this study. Firstly, we looked at the effect of N-additions on plant productivity and on the chemical composition of litter formed during the period in which the N-supply was experimentally increased ('new litter'). This contrasts with another type of study, in which the effect of N amendments on litter decay is studied in situations where the litter was formed during a period without additional N-supply ('old litter'). In those types of studies, positive effects (French 1988; Hunt et al. 1988), no effect (Van Vuuren and Van der Eerden 1992) or even a negative effect (Fog 1988) of N-addition on organic matter decay is found. Therefore, a clear distinction must be made between effects of N-addition on 'old' litter and on 'new' litter. The second point to be made is that we looked in this study at the potential decay rates of the plant litter (cf. Hogg 1993). Thus, we looked at the initial stages of decomposition under aerobic conditions and at a relatively high temperature (20 °C). As a result, the values we found are maximum estimates of decay rates. Further study is needed to see whether the observed differences in decay rates persist during later stages of decay when the easily decomposable organic matter has been broken down completely. Moreover, decay should be further studied when the litter is transferred to organic soil horizons which are below the water-table. As the decay rate of organic matter under anaerobic conditions is about two orders of magnitude lower than under aerobic conditions (Clymo 1984) it is questionable whether the observed differences in decay rates are still detectable.

The third point to be noted is that the effects observed in this study occurred at relatively high N-supply rates. However, due to the high internal N-circulation rates in Dutch ecosystems these supply rates are clearly within the N-availability range plant species experience in the Netherlands, i.e. with maximum values of 17–24 g N m⁻² year⁻¹ (Berendse 1990; Verhoeven et al. 1990). In a study area with very low atmospheric N-deposition rates (sub-Arctic Sweden) we detected productivity increases in a N-limited peatland at a much lower N-supply rate (2 g N m⁻² year⁻¹) (Aerts et al. 1992a).

In conclusion, this study provides evidence that increased levels of atmospheric N-deposition may affect the CO₂-sink function of peatlands, but that this effect is dependent on the nature of nutrient limitation. In peatlands where plant growth is N-limited, increased N-supply leads to an increase in the net accumulation of C. Under conditions of P-limited plant growth, however, the net accumulation of C will decrease. As plant growth in most terrestrial ecosystems is N-limited, increased atmospheric N-deposition will in general increase the CO₂-sink function of peatlands.

Acknowledgements Thanks are due to B. Beltman, M. van Oorschot, R. Scheffer and J.T.A. Verhoeven who commented on an earlier draft of this paper, and to M. Kortbeek-Smithuis who made the figures.

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