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Nitrogen Dioxide – a Gaseous Fertilizer of Poplar Trees

By

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With 4 Figures

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Summary

SCHMUTZ P., TARJAN J., GÜNTHARDT-GOERG M. S., MATYSSEK R. & BUCHER J. B. 1995. Nitrogen dioxide – a gaseous fertilizer of poplar trees. – Phyton (Horn, Austria) 35 (2): 219–232, 4 figures. – English with German summary.

Cuttings of a poplar clone (*Populus* × *euramericana* 'Dorskamp') were exposed to filtered air and to filtered air with 80 to 135 nl l^{-1} NO_2 added in climate chambers during 12 weeks. Three different levels of nitrogen fertilization were used, the lowest causing symptoms of nitrogen deficiency. NO_2 fumigation caused no visible injury to the plants. Fumigated plants showed elevated activity of nitrate reductase and higher leaf nitrogen concentrations relative to the control, indicating nitrogen assimilation from NO_2. Fumigation enlarged the foliar area and, at the lowest nitrogen supply from the substrate, elevated the net CO_2 assimilation rate. At the highest level of soil nitrogen supply, fumigation enlarged the width of xylem and bark tissue in the main stem. Fumigation had a stimulating effect on total biomass production during the exposure period. Thus, NO_2 acted as a nitrogen fertilizer, regardless of the nitrogen supply from the substrate. The results are discussed with regard to hypotheses concerning the impact of nitrogen oxides on forest ecosystems.

Zusammenfassung

SCHMUTZ P., TARJAN J., GÜNTHARDT-GOERG M. S., MATYSSEK R. & BUCHER J. B. 1995. Stickstoffdioxid – Ein Dünger: Versuche mit Pappeln. – Phyton (Horn, Austria) 35 (2): 219–232, 4 Abbildungen. – Englisch mit deutscher Zusammenfassung.

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Stecklinge eines Pappelklons (*Populus* × *euramericana* 'Dorskamp') wurden in Klimakammern in filtrierter Luft und in filtrierter Luft mit 80 bis 135 nl l^{-1} NO_2 während 12 Wochen angezogen. Drei verschieden hohe Stickstoffgaben wurden mit der Düngung verabreicht; die tiefste erzeugte bei den Pflanzen Mangelsymptome. Die Begasung mit NO_2 führte zu keiner sichtbaren Schädigung. Die Blätter begaster Bäume zeigten eine höhere Aktivität der Nitrat-Reductase und höhere Stickstoffgehalte als diejenigen der Kontrolle, was auf eine Assimilation des Stickstoffs aus NO_2 hinweist. NO_2 erhöhte die Gesamtfläche der Belaubung, und bei den Bäumen mit der niedrigsten Stickstoffdüngung zudem die CO_2-Assimilationsrate. Bei der höchsten Stickstoffdüngung führte NO_2 zu grösseren Dicken von Xylem und Rinde im Hauptstamm. Die Biomasse-Produktion der Bäume erhöhte sich durch die Begasung. NO_2 wirkte daher als Dünger auf die Pappeln, unabhängig von deren Stickstoffversorgung aus dem Dünger im Substrat. Die Ergebnisse werden im Zusammenhang mit Hypothesen über die Wirkung von Stickoxiden auf Waldökosysteme diskutiert.

Introduction

Nitrogen dioxide (NO_2), an important air pollutant in Central Europe, is considered as a potential threat to forest ecosystems (SCHULZE 1989). However, the results of experimental NO_2 fumigation on plants are still controversial: Inhibitory effects may be caused by cellular acidification, enhanced level of intracellular nitrite or radical reactions induced by NO_2 (Review ed. by WELLBURN 1990). Stimulating effects on plant growth and photosynthesis, particularly observed at low NO_2 concentrations, have been attributed to possible leaf fertilization by NO_2 (ROWLAND & al. 1987, WELLBURN 1990).

NO_2 is expected to undergo disproportionation to nitrate and nitrite in the liquid phase of the mesophyll (LEE & SCHWARTZ 1981). A nitrate assimilation system in leaves converts N from nitrate into organic N for biomass (WELLBURN 1990). Needles of spruce, fumigated with 15-NO_2, incorporated labelled N into amino acids (KATZ & al. 1989, VON BALLMOOS & al. 1993).

The response of plants to additional N input by atmospheric NO_2 may depend on their overall nutritional status. Whereas plants with N deficiency are expected to respond with additional growth, plants with a high N supply may become over-fertilized. This may lead to effects such as nutrient imbalances and excessive accumulation of nitrogen compounds and toxic waste products in leaves which, in turn, may cause premature leaf loss (NIHLGÅRD 1985, SCHULZE 1989).

In the present study with poplar trees we examined whether there was evidence for N incorporation from atmospheric NO_2 into biomass. We therefore measured the activity of nitrate reductase (NR) which is considered as the key enzyme in the N assimilatory pathway (RUNGE 1983). We also tested the 'over-fertilization' hypothesis by fumigating trees with differing soil N supply to compare their response to NO_2.

Abbreviations:

NR = nitrate reductase
LN = low N supply from the substrate (1.05 g N per pot)
MN = mid N supply from the substrate (3.15 g N per pot)
HN = high N supply from the substrate (6.3 g N per pot)

Materials and Methods

Cloned cuttings (13 cm long) of hybrid poplar (*Populus* × *euramericana* var. 'Dorskamp') were grown in 10 l plastic pots filled with quartz sand above a drainage layer of inert synthetic clay beads. The sand was covered by a thin layer of quartz gravel to reduce evaporation. The following five types of fertilizer were added to the sand (initial nutrient contents cf. Table 1): 1. Osmocote plus granules (15% N/10% P_2O_5/12% K_2O + micro nutrients), 2. Osmocote potassium granules (45% K_2O), 3. Osmocote urea granules (39% N), 4. Triple-Superphosphate granules and 5. Kieserit ($MgSO_4 \times H_2O$) granules. Three soil N treatments were set up by adding different amounts of Osmocote urea. The Osmocote granules were slow-release fertilizers (Sierra Chemical Europe, The Netherlands) with a release time of 5 to 6 months. The initial contents of the main nutritional elements per substrate volume are listed in Table 1. In the mid N (MN) treatment, the macro nutrients were present in a ratio which had permitted optimal growth of poplar in preliminary experiments. Water supply was kept non-limiting throughout the experiment.

Table 1
Initial contents of macro nutrients in the pots (mg l^{-1} sand mixture).

N regime	P	K	S	Mg	Ca	Fe	NO_3^--N	NH_4^+-N	total N
LN (low N)	98	221	119	37	147	1	55	50	105
MN (mid N)	98	221	119	37	147	1	55	260	315
HN (high N)	98	221	119	37	147	1	55	575	630

Immediately after potting, the cuttings were transferred into two walk-in climate controlled growth cabinets (9,7 m^2 each; BBC-York, FRG; 10 plants per soil N treatment and chamber). From each cutting, one shoot was allowed to grow out of a lateral bud. Plant growth continued for the subsequent twelve weeks, the duration of the experiment.

Photosynthetic photon flux density (PPFD) in the chambers was zero from 10:00 p.m. to 4:00 a.m. and about 800 umol m^{-2} s^{-1} at foliage height from 7:00 a.m. to 7:00 p.m. PPFD was changed in four hourly steps between the day/night regimes. Each chamber was illuminated by 25 lamps (Power Star HQI-E 1000 W, Osram). Air temperature and relative humidity followed a smooth diurnal course (min./max.: 12/20°C and 80/70%). Each chamber received filtered air (charcoal and Purafil) at a rate of 100 m^3 h^{-1} (wind speed in chamber approx. 0.5 m s^{-1}). NO_2 (from a flask containing 1% NO_2 and 99% nitrogen) was added to the air of one chamber. NO_2 concentration was monitored with a 'Nitrogen Oxide Analyzer Model 8840' (Monitor Labs Inc., USA) and adjusted by a mass flow controller according to the setpoints of a computer program. NO_2 concentration in the fumigation chamber followed a sinusoidal diur-

nal course (maxima at 9:00 a.m. and 9:00 p.m. = 135 nl l^{-1}, minima = 80 nl l^{-1}, mean = 100 nl l^{-1}, fumigation break between 12:00 p.m. and 1:00 a.m. due to technical reasons). The diurnal course of NO_2 was qualitatively similar to that in the air of rural surroundings of Zurich, Switzerland (BLEULER & LANDOLT 1986), but mean concentration was increased by a factor of about 6, thus being comparable to the highest daily means in Swiss cities (e.g. as measured in Lugano in December 1987; BUWAL 1988). The experiment was run twice, each time with a new set of plants (experiment 1 and 2).

The analyses of single leaves (3 to 4 weeks old) were carried out on five trees per fumigation/fertilization treatment. The total chlorophyll concentration (chlorophyll a and b) was optically determined with a SPAD-502 chlorophyll meter (Minolta, Japan) which was calibrated by comparison with chemical analysis of chlorophyll (LICHTENTHALER & WELLBURN 1983). The activity of nitrate reductase (NR, E.C. 1.6.6.1 and E.C. 1.6.6.2) was determined according to VON BALLMOOS & al. 1993 with the following modifications: 7 to 8 leaf discs (1.2 cm diameter) were excised and homogenized at 0°C with a micro-dismembrator (Braun, FRG) in 1.35 ml of the extraction medium described by VON BALLMOOS & al. 1993. After the addition of another 1.35 ml of extraction medium, 0.39 ml of the homogenate was incubated with 20 mM potassium nitrate, 150 µM NADH, 150 µM NADPH and 50 mM phosphate buffer pH 7.5 for 20 minutes at 30°C (the final volume being 1 ml). The reaction was stopped by adding 0.4 ml of 0.125 M zinc acetate. 20 minutes later, the mixture was centrifuged for 10 minutes at 14'000 × g. Nitrite was determined in the supernatant according to HAGEMAN & FLESHER 1960. NR activity was based on leaf area (µU/cm^2), 1 activity unit (1 U) being defined as 10^{-6} mole of substrate converted per minute.

Steady-state gas exchange measurements were conducted on whole leaves (four weeks old) attached to the stem using a climate-controlled cuvette system (Walz, FRG. Light intensity: 1100 µmol photons m^{-2} s^{-1}, leaf temperature: 17.5°C, leaf/air difference in the molar fraction of water vapor: 8 mmol mol^{-1}, CO_2 concentration: 340 µmol mol^{-1}; cf. MATYSSEK & al. 1991). Net assimilation rate was based on one-sided leaf area.

In the central internode of the main stems (3 trees per fumigation/fertilization treatment, experiment 1, MN treatment excluded) xylem radius and bark width were determined microscopically in cross sections.

Five trees per fumigation/fertilization treatment were used for whole-plant analyses. At the end of the 12-week fumigation, total foliage area was determined (Area Measurement System, Delta T Devices, GB). All plant organs were dried to constant weight at 65°C (3 days) and dry weight (biomass) was determined. In calculation of the root/shoot biomass ratio the stem section of the initially planted cuttings was excluded (cf. MATYSSEK & al. 1993). N concentration was measured with a C/N analyzer (Carlo Erba NA 1500). The other macro nutrients were determined by ICP-AES (Inductively Coupled Plasma Atomic Emission Spectroscopy).

The data were analyzed by multifactor analysis of variance, ANOVA, (STATGRAPHICS 1991) with NO_2 fumigation and soil N fertilization as factors. The significance level (p) of the factorial effects are presented as < 0.05, < 0.01 and < 0.001. For most parameters the experiment run had no significant effect on the response to fumigation and fertilization and therefore the data of the two experiments were pooled. However, for some parameters, the results of experiment 1 were not reproduced in experiment 2. These data had to be analyzed separately for the two experiments (Tables 2 to 5 show pooled data if not indicated otherwise).

Results

In all soil N treatments the activity of NR in leaves was higher in NO_2-exposed trees than in the corresponding control (Table 2). After four weeks of fumigation this effect was present as a trend, but after eight and twelve weeks it was significant (ANOVA: $p < 0.001$ for 12 weeks). The activity of NR after 12 weeks was as much as 5 times higher in NO_2-exposed trees than in the control (Fig. 1). The absolute values for NR activity were often highest in the HN treatment (Table 2).

Table 2

Nitrate reductase activity (NRA) of leaves in ($\mu U\ cm^{-2}$ and total chlorophyll concentration (Chl a+b) of the same leaves in ($\mu g\ cm^{-2}$ at various exposure times. Mean values; standard deviation in brackets. C = control, NO_2 = fumigated with NO_2.

	N treatment		MN treatment		HN treatment	
	C	NO_2	C	NO_2	C	NO_2
NRA 4 weeks	277 (119)	298 (68)	296 (103)	364 (107)	412 (165)	523 (198)
NRA 8 weeks	67 (39)	111 (48)	90 (35)	156 (53)	165 (81)	248 (79)
NRA 12 weeks	76 (42)	202 (99)	54 (52)	200 (92)	143 (112)	327 (224)
Chl a+b 12 weeks	29.1 (6.6)	32.5 (7.2)	36.8 (5.7)	38.1 (5.5)	41.0 (5.3)	44.9 (6.6)

Soil nitrogen supply increased nitrogen concentrations in all plant organs (Fig. 2, ANOVA: $p < 0.001$ for all organs). In the control trees of the high N treatment, the values in the leaves were in the range of the minimum values for poplar cited by FIEDLER & al. 1973. Trees fumigated with NO_2 had significantly higher leaf and root N concentration than control trees (Fig. 2, ANOVA: $p < 0.01$ for both organs). There was no significant NO_2 effect on the N concentrations in the main stems or cuttings.

Whole-plant N content was calculated from N concentration and biomass data (Table 4). The values for MN and HN trees were two and three times higher than for LN trees, respectively. Soil N supply for the MN treatment was five times and, for the HN treatment, eleven times higher than for the LN treatment. Therefore, it seems that the additional N provided in the MN and HN treatments was only partially used by the trees.

In NO_2-exposed trees, a higher proportion of total N content was located in the foliage than in control trees (Table 4, ANOVA: $p < 0.01$).

Table 3

Leaf parameters of the exposed trees. All areas are in cm^2 (specifications in second lines of first column); net CO_2 assimilation rate at ambient CO_2 concentration in µmol m^{-2} s^{-1}; chlorophyll concentrations of the same leaves in µg cm^{-2}. Mean values; standard deviation in brackets. C = control, NO_2 = fumigated with NO_2

	LN treatment		MN treatment		HN treatment	
	C	NO_2	C	NO_2	C	NO_2
foliage area total	2219 (439)	2762 (481)	4423 (1388)	5203 (1413)	5627 (1223)	7222 (1675)
foliage area main stem	2160 (370)	2599 (351)	3310 (692)	3720 (350)	3783 (712)	4684 (271)
foliage area branches	59 (84)	163 (244)	1113 (963)	1482 (1318)	1844 (732)	2538 (1431)
leaf number main stem	37 (4)	38 (3)	42 (4)	44 (4)	41 (3)	44 (3)
mean leaf area main stem	58 (8)	68 (5)	79 (14)	86 (8)	91 (13)	108 (4)
net CO_2 assimilation rate	10.5 (1.4)	12.0 (0.9)	-	-	16.2 (1.4)	15.5 (2.0)
Chlorophyll a+b	43.4 (6.1)	47.4 (4.2)	-	-	59.0 (5.0)	56.6 (4.3)

Leaf concentrations of calcium, magnesium and phosphorus (Table 4) were within the range considered by FIEDLER & al. 1973 as normal for poplar leaves. There was no significant effect of NO_2 exposure. Leaf concentration of potassium in MN and HN trees were reduced by about 45% compared to LN trees (Table 4, ANOVA: $p < 0.001$) and were about 25% below the concentration range cited by FIEDLER & al. 1973. K concentrations of LN trees were within that range. There was no significant NO_2 effect. Due to the increase of N concentration, however, NO_2 fumigation significantly reduced the K/N concentration ratio in leaves (Table 4, ANOVA: $p < 0.001$).

The area-based net CO_2 assimilation rate at ambient CO_2 concentration (A_{amb}) was significantly higher in the HN than in the LN treatment (Table 3; ANOVA: $p < 0.001$). Fumigated trees of the LN treatment showed significantly higher values for A_{amb} than the corresponding controls (ANOVA: $p < 0.05$). No fumigation influence was found in the HN treatment (Table 3). Total chlorophyll concentration per leaf area (chlorophyll a and b) was measured in the same leaves as A_{amb}. No significant fumigation effect was found (Table 3). Young leaves (those in which NR activity after 12 weeks of NO_2 exposure was measured), however, showed a significantly

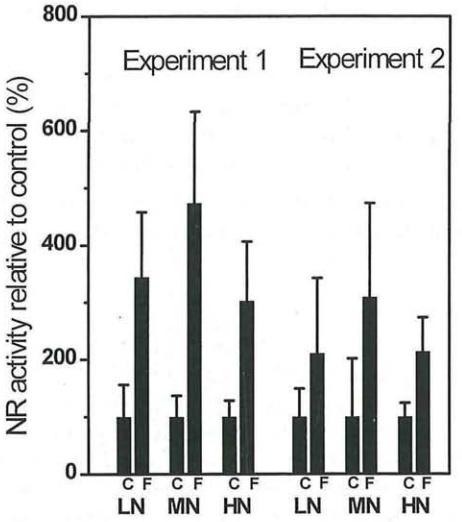

Fig. 1. Nitrate reductase activity in leaves, based on leaf area, measured after 12 weeks of fumigation. Controls are set to 100% and data for fumigated plants are shown relative to the corresponding controls. Mean values (columns) and standard deviations (lines) of five replicates are shown. C = Control, F = Fumigated with NO_2; LN = low, MN = mid and HN = high N supply from the soil.

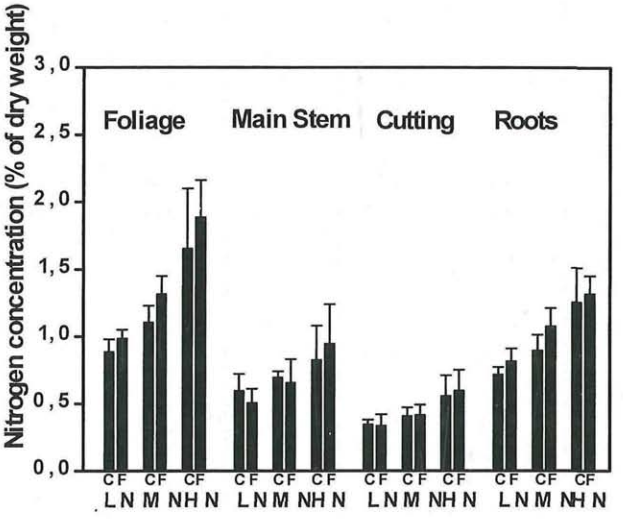

Fig. 2. Total nitrogen concentrations in main stem foliage, main stem, cutting and roots. The data of Experiment 1 and 2 are pooled. Mean values (columns) and standard deviations (lines) of ten replicates are shown.
C = Control, F = Fumigated with NO_2; LN = low, MN = mid and HN = high N supply from the soil.

higher chlorophyll concentration than the corresponding controls (Table 2; ANOVA: $p < 0.05$).

Total foliage area was significantly higher in fumigated trees than in controls for all soil N treatments (Fig. 3; ANOVA: $p < 0.01$). It was also positively correlated with soil N supply (ANOVA: $p < 0.001$). Both the leaves on the main stem and those on branches contributed to the higher foliage area of the fumigated trees. Leaves on the main stem responded to NO_2 by increased mean single leaf areas rather than by increased number (Table 3).

Table 4

Biomass (dry weight) in g; root/shoot biomass ratio (dimensionless); whole-tree biomass/foliage area (bm./fol.area) in mg cm^{-2}; branch biomass/main stem biomass (branch/ms) in %; whole plant N content in g; N content in foliage relative to whole-plant N content in %; concentrations of P, Ca, Mg and K in foliage in promilles; K/N concentration ratio in leaves (dimensionless). Results of experiment 1 and 2 pooled if not indicated otherwise. Mean values; statistical evaluation refer to 'result' section.
C = control, NO_2 = fumigated with NO_2.

	LN treatment		MN treatment		HN treatment	
	C	NO_2	C	NO_2	C	NO_2
biomass:						
–whole	72	86	121	128	116	138
–shoot	41	50	76	82	79	96
–cutting	9	10	11	12	10	11
–roots	21	25	33	34	28	32
root/shoot:						
–exp. 1	0.52	0.51	0.52	0.46	0.40	0.35
–exp.2	0.52	0.50	0.39	0.38	0.31	0.32
bm/fol. area	32	31	28	25	21	19
branch/ms						
–exp. 1	0	0.04	0.14	0.14	0.32	0.20
–exp. 2	0.04	0.06	0.32	0.39	0.38	0.51
whole plant N content	0.51	0.66	1.10	1.34	1.51	1.99
rel. N content leaves	49.1	51.3	51.0	53.6	57.5	58.5
P conc.	1.7	1.7	1.5	1.4	1.5	1.5
Ca conc.	13.1	12.8	15.7	15.0	16.9	16.2
Mg conc.	3.1	3.3	3.8	3.6	4.1	3.9
K conc.	7.7	7.5	4.5	4.3	4.3	4.2
K/N	0.88	0.76	0.41	0.33	0.27	0.23

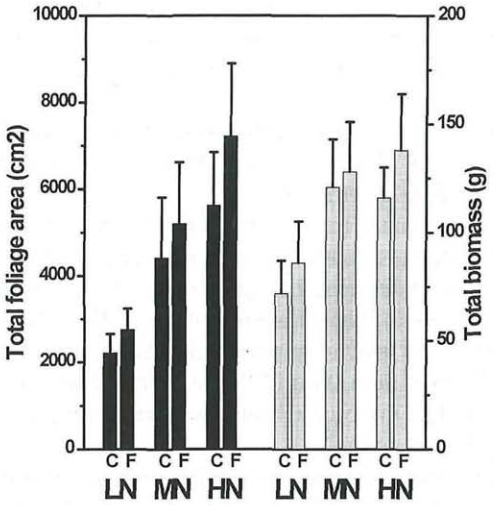

Fig. 3. Total foliage area (left) and total biomass (right). The data of experiment 1 and 2 are pooled. Mean values (columns) and standard deviations (lines) of ten replicates are shown. C = Control, F = Fumigated with NO_2;
LN = low, MN = mid and HN = high N supply from the soil.

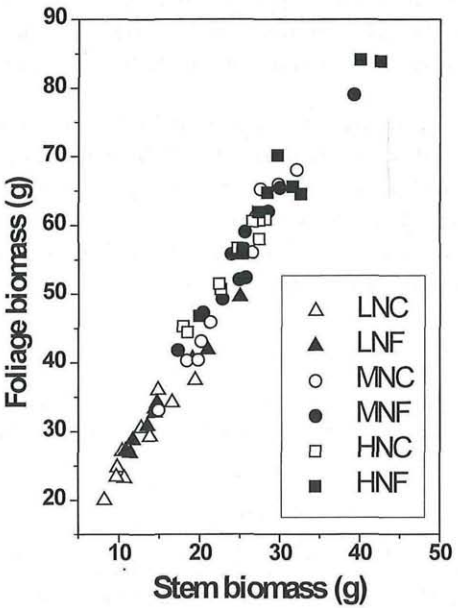

Fig. 4. Total foliage biomass in relation to stem biomass (including branches). The single-tree data of experiment 1 and 2 are pooled. C = Control, F = Fumigated with NO_2;
LN = low, MN = mid and HN = high N supply from the soil.

Soil N supply had a positive effect on total biomass production (ANOVA: $p < 0.001$). MN trees produced approx. 60% more biomass than LN trees. No significant differences occurred between the MN and HN treatment (Fig. 3).

NO_2 fumigation resulted in higher total biomass of the trees (Fig. 3; ANOVA: $p < 0.01$). The effect occurred at all soil N levels but was smaller in MN than in the other treatments.

The root/shoot biomass ratio was lowered with increasing soil N supply (Table 4; ANOVA: $p < 0.001$ for both experiments). The ratio was significantly lower in NO_2-exposed than in control trees in the first experiment (ANOVA: $p < 0.05$), with the exception of the LN treatment. There was no difference in the second experiment (Table 4).

Stem (including branches) and foliage biomass were closely correlated to each other (Fig. 4). Obviously, biomass partitioning between stem and foliage was not affected by NO_2.

The number of branches increased with increasing soil N supply (data not shown). Consequently, a higher proportion of the above-ground biomass was invested into branches and the branch/main stem biomass ratio increased (Table 4, foliage included). The latter ratio was not affected by NO_2 exposure.

The ratio of total biomass/total foliage area was highest in the LN treatment and decreased in trees with increasing soil N supply (Table 4; ANOVA: $p < 0.001$). NO_2 fumigation lowered the biomass/foliage area ratio as well (ANOVA: $p < 0.05$), the effect being small compared to the soil N effect.

Fumigated trees of the HN treatment had a larger main stem radius than the corresponding control (Table 5). The unchanged relative bark width (as percentage of the main stem radius) shows that in the HN treatment both xylem and bark responded similarly to NO_2 (Table 5). Compared to the LN treatment, the main stem radius was larger in the HN treatment at a smaller relative bark width (Table 5).

Table 5

Stem radius in mm and relative bark width in % of stem radius. Mean values of three replicates; lowest and highest value in brackets. C = control, NO_2 = fumigated with NO_2.

	LN treatment		HN treatment	
	C	NO_2	C	NO_2
stem radius	1.82 (1.75-1.93)	1.74 (1.61-1.82)	2.09 (1.93-2.27)	2.46 (2.44-2.48)
relative bark width	46.6 (43.6-48.8)	51.0 (47.5-53.7)	41.1 (35.5-46.8)	41.9 (39.8-43.4)

Discussion

Nitrate reductase catalyzes the reduction of nitrate to nitrite and plays a key role in the assimilation of N from nitrate. Biosynthesis of the NR enzyme is induced by nitrate (substrate induction; RUNGE 1983, WELLBURN 1990). NO_2 is expected to produce nitrate in the mesophyll (LEE & SCHWARTZ 1981) and has been shown to induce NR in leaves (WELLBURN 1990).

In the present study, NO_2-exposed poplar trees showed considerably higher NR activities in their leaves than the control. The high NR activity in the presence of NO_2 demonstrated the potential of the leaves to assimilate N from this gas. N fertilization had no effect on the NO_2-induced increase of NR activity.

Was N from NO_2 incorporated into biomass ? Overall N concentration in leaves was higher in fumigated than in control trees, indicating N uptake from atmospheric NO_2. Whole-plant content of N increased even more by NO_2 exposure. Fumigated trees showed a slight shift in N distribution in favor of foliage. Assuming that the difference in whole-plant N content between fumigated and control trees originated entirely from NO_2, absorption rates of NO_2 per shoot biomass were calculated (mean shoot dry weight during the exposure was approximated as being 50% of the final dry weight). The results are 0.07, 0.07 and 0.12 mg N g^{-1} shoot dry weight day^{-1} for low N supply from the substrate (1.05 g N per pot), mid N supply from the substrate (3.15 g N per pot) and high N supply from the substrate (6.3 g N per pot) trees, respectively. These rates are similar to 0.04 mg N g^{-1} dry weight day^{-1} obtained by exposing barley to 33 nl l^{-1} NO_2 (JENSEN & PILEGÅRD 1993).

LN trees showed symptoms of N limitation, such as low N and chlorophyll concentrations in leaves and a low branching rate. Additional N supply from the soil reduced these symptoms. In control trees of the MN and HN treatments leaf K concentrations were low (cf. FIEDLER & al. 1973). However, growth limitation by K seems unlikely, since biomass production could still be stimulated by additional N input from NO_2. The uptake of Ca, Mg and P was sufficient for all treatments (cf. FIEDLER & al. 1973).

The most obvious NO_2 effect at the leaf level was the considerable enlargement of total foliage area, mainly due to the higher mean area of single leaves. Photosynthesis correlated much less with NO_2 exposure. The response of foliage growth is apparently the result of leaf fertilization by NO_2, as has been proposed for barley by ROWLAND & al. 1987.

This response of the foliage finally led to higher biomass production, regardless of soil N supply. These findings contrast with results for barley, in which the response to NO_2 decreased with increasing N fertilization (ROWLAND & al. 1987).

The ratio of total biomass to total foliage area – a measure of biomass production per unit of leaf area – was reduced by increasing soil N supply and by NO_2 fumigation. Since the trees were still growing at the time of biomass harvesting, part of the foliage had been produced recently. Presumably, the higher assimilating area of well-fertilized trees had not yet had time to be reflected in an equally high biomass.

The biomass ratio of root to shoot was negatively correlated with the N input from the soil, which was in accordance with the expectations based on other reports (Review: WARING 1991). NO_2 lowered this ratio in the first experiment, indicating its role as a N fertilizer. However, the effect did not occur in the second experiment. At the shoot level, a close biomass correlation between stems and foliage existed. Apparently, each unit of green biomass required a constant equivalent of above-ground non-green biomass.

It has been proposed that NO_2 may contribute to a general over-fertilization of forests and other ecosystems due to elevated N deposition from anthropogenic sources (NIHLGÅRD 1985). According to this hypothesis, the gas enters the plants by the foliage and other above-ground parts (SCHULZE 1989) and acts as an additional nutrient source. This may result in imbalances between N and other nutrients, such as magnesium or potassium. High concentrations of N in non-protein storage forms (such as amino acids) in leaves may lead to premature leaf abscission (NIHLGÅRD 1985).

In our experiments, poplar responded to NO_2 fumigation with the accumulation of additional N and stimulated growth. However, this accumulation did not lead to premature leaf loss or any other symptoms of leaf injury. Although NO_2 exposure reduced the K/N concentration ratio in leaves, no symptoms of K deficiency, such as an increased wilting tendency (BERGMANN 1992), were apparent.

In the present study, NO_2 acted as a fertilizer. However, as a fast growing tree, poplar may have a high potential demand for N. In a field study, AL GHARBI & HIPKIN 1984 found higher foliar activities of NR in *Populus* species than in *Fagus, Quercus* and *Carpinus*. It remains to be seen, whether these findings reflect differences in N assimilation capacities between tree genera. If so, NO_2 may have an effect on competition in forest ecosystems.

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Recensio

LEUTHOLD Barbara 1994. Vegetations- und Standortsveränderungen auf von Hochwasser überschlickten Streuwiesen. – Veröffentlichungen des Geobotanischen Institutes Rübel, Zürich. H. 121. – 8°, 83 Seiten, mit 31 Figuren und 12 Tabellen im Text und 4 Beilagen, broschürt, sfr 55,–. – ISSN 0254-9433

Heft 105 der Veröffentlichungen beinhaltet die Ergebnisse des pflanzenökologischen und limnologischen Ist-Zustandes des bekannten Reussdeltas im Kanton Uri/Schweiz, worüber in Phyton referiert wurde. Die Überschwemmungen und starken Überschlickungen der Riedwiesen im Reussdelta im Jahre 1987, wurden zum Anlaß genommen, um die Sekundär-Sukzession der überschlickten Streuwiesen zu untersuchen. Das Hochwasser lagerte im Reussdelta bis zu einem halben Meter hohe Sedimente ab. Die Vegetationsaufnahmen wurden durch Zeigerwertanalysen, Grundwasserstandsmessungen und Bodenanalysen ergänzt. Obwohl die Untersuchungen sich nur über einen Zeitraum von drei Jahren erstreckten, wurde die Überschlickung aus botanischer Sicht negativ bewertet. Mehrere Orchideen (z.B. *Traunsteinera globosa,* einige Orchis-Arten) sowie das Primulo-Schoenetum mit *Rhynchospora alba* sind nach der Überschlickung gänzlich verschwunden. Am besten wurden die Schlickablagerungen von Arten mit unterirdischen Ausläufern überstanden wie z.B. von *Phragmites communis, Equisetum palustre, Agrostis gigantea.* Für den Weiterbestand des Primulo-Schoenetum wird ein Grenzwert von 5 cm Schlick angegeben, für die Klein-Seggenriede eine Schlickmächtigkeit von 10 cm. Die größte Überschlikkung von 20–25 cm erträgt die Hochstaudenriede (Valeriano-Filipenduletum). Nach den Bodenanalysen kann die Überschlickung nicht als Düngung gewertet werden. Als entscheidender Faktor der Standortsveränderungen wird der niedrige Humusgehalt und das damit verbundene geringe Wasserhaltevermögen des Oberbodens angenommen.

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