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Plant Effects on Variability of Denitrification N Emissions in Cultures of Potted Ornamental Plants

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Summary

It was the aim of this study to investigate denitrification N loss and plant effects on its variability in cultures of potted ornamental plants. Experiments were conducted in flow-through chambers with plants of *P. zonale* 'Grand Prix' and *E. pulcherrima* 'Sonora Red' grown in peat substrate. Acetylene was applied at 5 vol.% to inhibit reduction of N_2O. N emissions from planted pots started to evolve 2 to 4 hours after each irrigation event and followed a peak shaped curve. Variability in height and width of peaks was high among replications. N emissions strongly depended on high substrate water content; they ceased when water content dropped below a threshold value. Permanent flooding as well as reduction of plant transpiration retarded the decrease in water content and increased the duration of N emissions. Plant transpiration showed a close relationship to vapour pressure deficit (vpd) of air and mean N losses showed good correlation to vpds. It was concluded that plant transpiration determined the duration of denitrifying activity. With increasing plant age and size the duration of N emissions shortened but plants also seemed to increasingly stimulate N emissions. Emissions from potted eight-week old *P. zonale* evolved sooner and reached a maximum that was more than twice as high as those of four-week old plants. Possible reasons for stimulating and reducing plant effects on denitrification are discussed.

Zusammenfassung

Einflüsse der Pflanze auf die Variabilität der N-Emissionen durch Denitrifikation in Zierpflanzen-Topfkulturen. Das Ziel der Untersuchungen war, N-Verluste durch Denitrifikation sowie den Einfluss der Pflanze auf die Variabilität der Verluste in Zierpflanzen-Topfkulturen zu erforschen. Dazu wurden in Durchflusskammern Versuche mit in Torfsubstrat kultivierten Pflanzen der Arten *P. zonale* 'Grand Prix' und *E. pulcherrima* 'Sonora Red' durchgeführt. Acetylen wurde mit 5 vol.% eingesetzt, um die Reduktion von N_2O zu hemmen. Zwei bis vier Stunden nach jedem Bewässerungsereignis begannen N-Emissionen aus den bepflanzten Töpfen zu entweichen. Die Emissionen folgten einem Peak-förmigen Verlauf. Die Variabilität der Höhe und Breite der Peaks war zwischen den Wiederholungen hoch. Die N-Emissionen zeigten eine starke Abhängigkeit von einem hohen Wassergehalt und endeten erst, wenn dieser unter einen Grenzwert abfiel. Dauerhafte Anstaubewässerung sowie die Einschränkung der Transpiration verzögerten das Absinken des Wassergehalts und erhöhten die Dauer der N-Emissionen. Die Transpiration der Pflanzen zeigte eine enge Beziehung zum Wasserdampfdruckdefizit (vpd) der Luft und die mittleren N-Verluste waren mit dem vpd korreliert. Daraus wurde geschlossen, dass die Transpiration der Pflanze die Dauer der denitrifizierenden Aktivität bestimmte. Mit steigendem Alter und steigender Größe der Pflanzen verkürzte sich die Dauer der N-Emissionen, gleichzeitig schienen die Pflanzen die N-Emissionen zunehmend zu fördern. Emissionen aus Substrat mit acht Wochen alten *P. zonale* entwichen früher und erreichten ein mehr als zweifach höheres Maximum als die aus Substrat mit vier Wochen alten Pflanzen. Mögliche Ursachen stimulierender und hemmender Pflanzeneffekte auf die Denitrifikation werden diskutiert.

Key words. denitrification – horticulture – N loss – plant effect – pot plants

Introduction

Nitrate is mainly lost from plant production systems in two ways, by denitrification and by leaching. The physiology of denitrification has become well known through laboratory research but nevertheless knowledge of environmental parameters does not allow reliable prediction of denitrification at field scale (GROFFMAN 1991; MOSIER et al. 1996). Although denitrification is mainly controlled by anaerobiosis and availability of nitrate and carbon, it is a very complex and dynamic process which is affected by a multitude of interacting physical, chemical, and biological soil parameters (TIEDJE et al. 1989; GROFFMAN 1991).

The sensitivity of the denitrification process to spatial or temporal changes in the soil environment causes the characteristically high variability of gaseous N emissions (FOLORUNSO and ROLSTON 1984). Tracing back the causes of high variation in denitrification requires thorough soil analysis. Consequently, the transfer of knowledge on denitrifying activity from soil to soil or from soil to other growth substrates is limited.

Most research on denitrification has focused on agricultural soils, but it is the objective of this study to investigate denitrification in cultures of potted ornamental plants grown in peat substrate. In this growing system it was suggested that denitrifying conditions and the resulting variability of N loss may be strongly controlled by plants because they are confined to a very small substrate volume relative to plants grown in the field. With many ornamental plants, potted substrate is usually thoroughly rooted within two to four weeks after planting. Thus, conditions in the substrate, are considered to be strongly influenced by plant activity.

In the literature, stimulating as well as reducing effects of plants on denitrification are described. Stimulation of denitrifying activity in planted soils has been related to oxygen consumption by roots and to rhizodeposition, which increase anaerobiosis and availability of carbon to denitrifiers (SMITH and TIEDJE 1979; WOLLERSHEIM et al. 1987; TROLLDENIER 1989; MAHMOOD et al. 1997). Reducing effects of plants on denitrification, on the other hand, were attributed to plant nitrate uptake and the resulting substrate deficiency for nitrate respiration (SMITH and TIEDJE 1979; RYDEN 1983; MAHMOOD et al. 1997). Additionally, plants may control denitrification by water uptake, leading to increased substrate aeration. This effect on denitrifying conditions was considered to be especially strong in horticultural pot plant production because of frequent irrigations or fertigations, which are necessary due to the limited substrate volume per plant and the resulting low water reserve per pot. Soil or substrate water content is of great importance for denitrification because of its influence on air filled pore space and oxygen availability. This is evidenced by many reports in the literature, where the highest peaks of N emissions from soil were recorded after rainfall or irrigation events (e.g. RYDEN and LUND 1980; ROLSTON et al. 1982; SEXTONE et al. 1985; BRONSON and MOSIER 1993) and denitrification N loss was positively correlated with soil water content (RYDEN 1983; LINN and DORAN 1984; WEIER et al. 1993; SHELTON et al. 2000).

Thus, experiments were conducted to investigate denitrification and sources of its variability in cultures of potted ornamental plants. The research focused on plant effects on dynamics, variability, and quantity of denitrification N loss.

Materials and Methods

Abbreviations

vpd – vapour pressure deficit ; vol.% – volume percent; wfps – water filled pore space.

Plant material and substrates

Plants of *Pelargonium zonale* 'Grand Prix' and *Euphorbia pulcherrima* 'Sonora Red' were grown in peat based substrate (340 mL plastic pots) containing 1 g L^{-1} of a soluble, full compound fertilizer (Flory3, Euflor: 15 % N in form of NO_3 (4,5 %) and NH_4 (10,5 %), P_2O_5 (10 %), K_2O (15 %), MgO (2 %) and trace nutrients). The peat content of the substrates was either 100 vol.% or 80 vol.%. Additional components were compost or cocopor. In line with horticultural practice, plants were fertigated during cultivation with a solution containing 1 g L^{-1} of the above-mentioned fertilizer. Plants were grown for at least four weeks before experiments took place to guarantee rooting of the substrate. For each experiment, plants of the same species and set were used, i.e. plants were of the same age and of similar growth. Only when the effect of plant age on N emissions was investigated were four and eight week old plants of *P. zonale* used in the same experiment.

Experimental setup for denitrification measurement

For denitrification measurement in the greenhouse, pots were locked into flow-through chambers, while the plant shoots remained outside the chambers. The chambers of 12 litre volume were aerated with an air stream of 50 L h^{-1} plus 5 vol. % acetylene (C_2H_2) to inhibit reduction of N_2O (YOSHINARI et al. 1977). Inhibition of the reduction of N_2O to N_2 was necessary because N_2O unlike N_2 can be readily measured by gas chromatography. For detailed description of the assay system see AGNER (2003). Treatment with 5 vol. % C_2H_2 within the chambers started two hours before the irrigation event, which was the defined start of the experiment. pots were flood irrigated for two hours with 1 litre of a 150 mg NO_3-N solution. Only in one experiment, in which the effect of permanent flooding on denitrification was investigated, did the fertigation solution remain in the chambers throughout the whole experiment.

Starting from the end of irrigation, air samples were taken with syringes topped with gauge needles from silicon tubes at the air outlet of the chambers every two to four hours until N_2O emissions ceased.

Reduction of transpiration

When the effect of reduced transpiration on N emissions was being investigated, plants were covered with cut open plastic bags that allowed air exchange but nevertheless increased relative humidity beneath the plastic cover.

Analysis of N_2O

The analysis of N_2O in all the air samples was performed by a gas chromatograph (Chrompack 9001) with an electron capture detector (ECD) according to a method described by MOSIER and MACK (1980).

Determination of substrate water content

During denitrification measurement, every four to eight hours, pots were taken from the chambers and

weighed. At the end of the experiment, plants were harvested and the fresh weight of the shoot and of the rooted substrate was determined. Then, the substrate was dried at 105 °C and weighed again. Water content (vol. %) was calculated from pot volume, fresh weight of shoot, dry weight of rooted substrate, and fresh weight during the experiment.

Determination of air filled pore space

The air filled pore space was calculated by subtracting the water content (vol. %) from the total pore space. The total pore space was determined by means of the 'Quick-Method' described by WREDE (2001).

Determination of vapour pressure deficit (vpd)

Temperature and relative humidity were determined during denitrification measurements. Both values were used to calculate the vapour pressure deficit (MURRAY 1967; MALBERG 2002):

$vpd = e(T) - e$

$e(T) = 0.6108\exp[17.27*T/(T+237.1)]$

$e = e(T) * rh/100$

vpd = vapour pressure deficit [kPa]

e = vapour pressure [kPa]

T = Temperature [°C]

e(T) = saturation vapour pressure [kPa]

rh = relative humidity [%]

Statistics

Statistics were performed using the SAS package. Measurements were conducted with six replications per treatment.

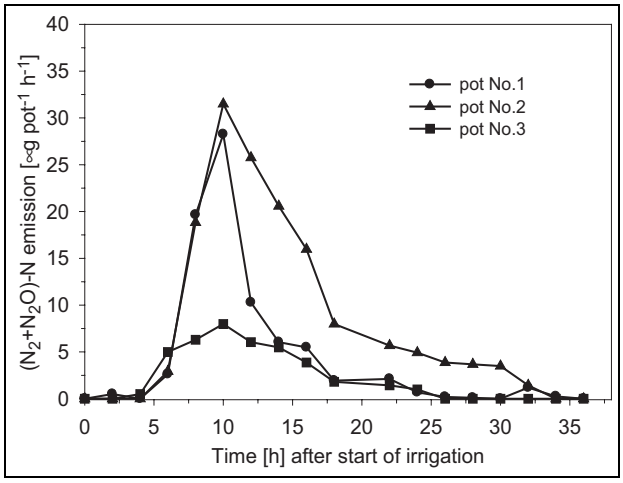


Fig. 1. (N_2+N_2O)-N emissions from a peat substrate planted with *P. zonale* following irrigation (5 vol.% C_2H_2).

Results

Course of N emissions

When denitrification N loss was measured in flow-through chambers from planted pots, N emissions always followed the same pattern (Fig. 1). Two to four hours after the beginning of irrigation N_2O started to be emitted. Emissions increased more or less sharply until they reached a maximum and then decreased again towards zero. The end of emissions was often observed 26 to 34 hours after irrigation. Although the pattern was the same, the height and also the width of the peaks differed among pots (Fig. 1). Consequently, total N loss showed the typically high variability of denitrification measurements.

Effect of substrate air and water content on denitrification

To investigate the causes of the observed variability, the substrate air and water content of a planted peat substrate were measured in addition to (N_2+N_2O)-N emissions after irrigation (Fig. 2). The mean N emissions out of six replicates followed a peak shaped curve and showed high variability. The mean water content of the substrate decreased steadily from the end of irrigation and with time its standard deviation increased. As

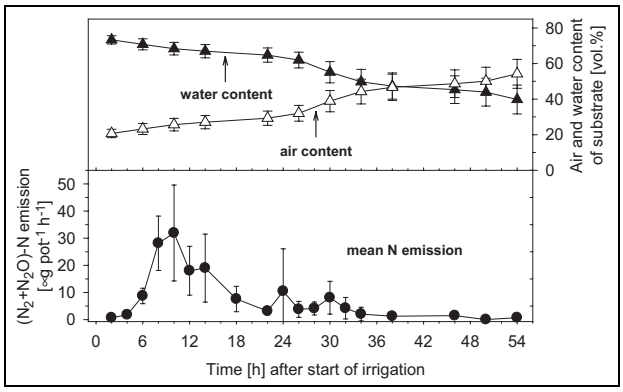


Fig. 2. (N_2+N_2O)-N emission rate, water and air content following irrigation of a peat substrate planted with *P. zonale* (5 vol.% C_2H_2), n=6.

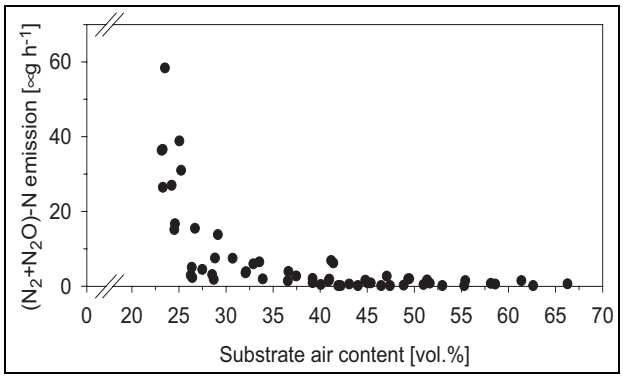


Fig. 3. (N_2+N_2O)-N emission rate depending on air filled pore space of a peat substrate planted with *P. zonale* (5 vol.% C_2H_2).

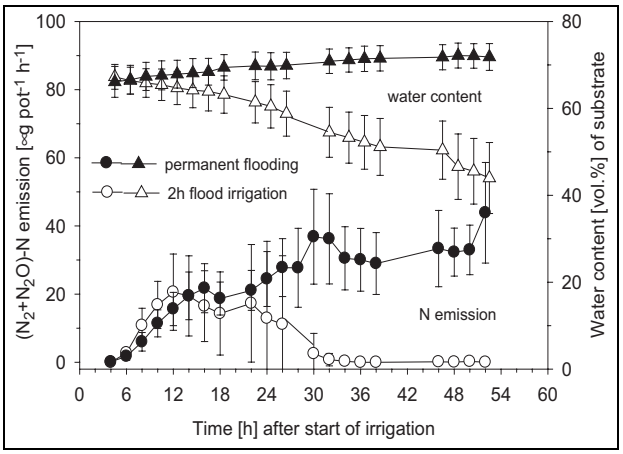


Fig. 4. (N_2+N_2O)-N emission rate and water content of peat substrate planted with *E. pulcherrima* following irrigation (2 h) or during permanent flooding (5 vol.% C_2H_2), n=6.

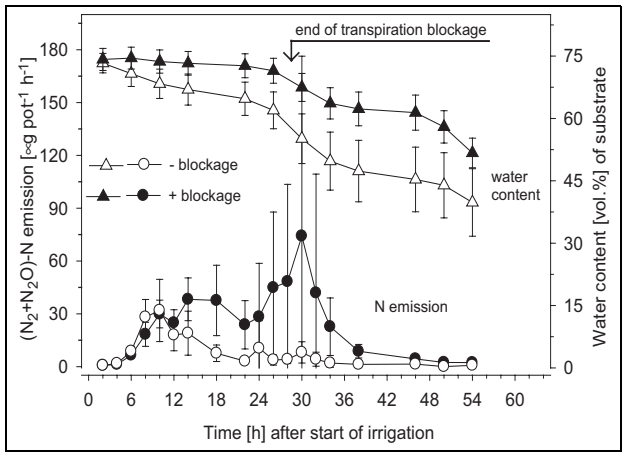


Fig. 5. (N_2+N_2O)-N emission rate and water content of a peat substrate planted with *P. zonale* following irrigation with or without blockage of transpiration (5 vol.% C_2H_2), n=6.

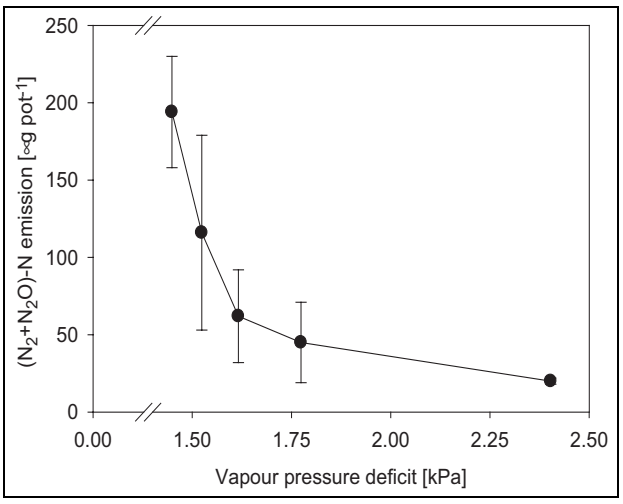


Fig. 6. (N_2+N_2O)-N emissions after irrigation by pots of *P. zonale* planted in peat substrate as affected by vapour pressure deficit, n=6.

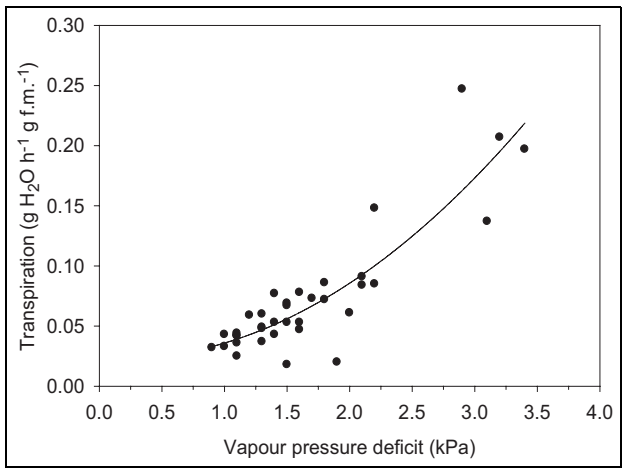


Fig. 7. Relationship of vapour pressure deficit and transpiration of *P. zonale* plants.

the air content was the reflection of the water content, it steadily rose after irrigation.

When N emissions were related to substrate air content the result was that below an average air content of 30 vol. % N was emitted at rates varying from 0 to 60 µg pot^{-1} h^{-1} (Fig. 3). Yet above 30 vol. % air no significant emissions occurred at all. To confirm the positive correlation between water content and N emission, N losses at different substrate water contents were measured. Variation of water content was obtained by short-term irrigation (2 h) and permanent irrigation (Fig. 4). After short-term irrigation of two hours substrate water content steadily decreased, while that of the continuously irrigated substrate slightly increased. N emissions of both treatments did not differ much at first. But, after 22 hours emissions of the short-term irrigated pots started to decrease while emissions of the permanently flooded pots further increased and did not cease until the end of the experiment.

Another approach to the variation of substrate water content was to vary the water consumption of plants, since the decrease in water content after irrigation is mainly due to transpiration by plants. Fig. 5 shows that at first blockage of transpiration by a plastic cover did not affect N emission rates. But after 10 h, when emissions of the control treatment without transpiration blockage decreased, those of the inhibition treatment still rose and only sank when the transpiration blockage was relieved after 28 hours. The water content of the substrates behaved accordingly. In the treatment without inhibition of transpiration it decreased rapidly, while in the treatment with reduced transpiration it sank only slightly until the end of transpiration blockage.

In this experiment, transpiration proved to be an important factor influencing denitrification via water and air content of the substrate. Thus, gaseous N loss of *P. zonale* pots strongly declined with increasing vapour pressure deficit (Fig. 6), since transpiration was enhanced (Fig. 7). The data was obtained during denitrification measurements under different weather conditions (different solar radiation, temperature, vpd). Nev-

ertheless, there was some variation in N loss that did not correspond to vapour pressure deficit, indicating that climate was not the only factor controlling denitrification in planted substrates.

Effect of plant age on N emissions

It was suggested that variation of plant size may contribute to variability of N emissions because it affects transpiration through size of leaf area and substrate conditions through root density. To obtain two uniform groups of plants differing in plant size, four and eight week old plants of *P. zonale* were used for simultaneous measurement of denitrification N loss (Fig. 8). Gaseous N emissions from the older plants increased steeply after irrigation, reached a maximum after eight hours, then declined just as steeply as they rose and finished after 14 hours of incubation. The course of emissions from the younger plants was more gently, rise and decline were not as steep and the maximum emission rate was only half as high as of the older plants. However, emissions from the pots of the younger plants lasted for a longer period and ceased only 24 hours after irrigation, since the younger plants did not reduce substrate water content as rapidly as the older plants (Fig. 8). Regardless of plant age, emissions stopped at the same threshold for water content (about 54 vol.%). In spite of the obvious difference in the course of N emissions, mean emissions per pot did not differ significantly.

Discussion

Effect of substrate air and water content on denitrification

The flow-through system allowed us to observe the dynamics of denitrification from undisturbed samples of planted substrate (Fig. 1, 2). N emissions were obviously related to the irrigation event, as they increased significantly only a few hours after irrigation. The duration of the denitrification event seemed to be determined by oxygen availability. Right after irrigation, the air filled pore space of the substrate was at its minimum, but it steadily increased during time following irrigation. N emissions were only observed as long as the

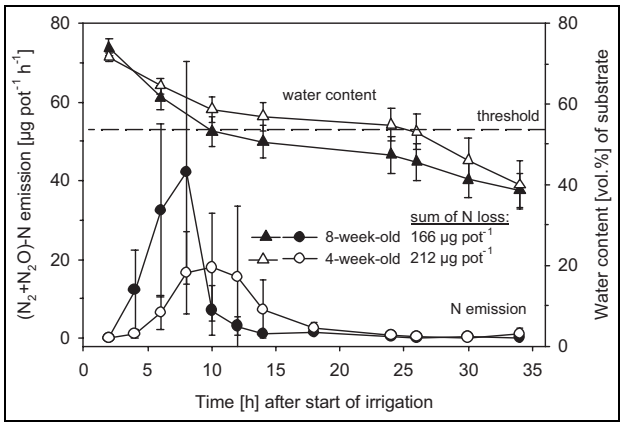


Fig. 8. Influence of plant age on (N_2+N_2O)-N emissions and substrate water content of potted *P. zonale* plants following irrigation (5 vol.% C_2H_2), n=6

average air content of the substrate was below 30 vol.% (Fig. 3). The dependence of denitrification on low air filled pore space was confirmed when return of air into the substrate was impeded by permanent flooding (Fig. 4). Then, N emissions did not cease, in contrast to emissions from the control treatment, which decreased when substrate water content became smaller after irrigation. The above observations are in accordance with the literature. SEXTONE et al. (1985), for example, reported rising N emission rates from soils after irrigation or rainfall events, which reached a maximum after three to five hours and then declined again to the pre-irrigation level. Similar observations were made by RYDEN and LUND (1980), who also showed the promoting effect of low soil water suction on N emissions. The positive relationship between soil water content and denitrification N emissions has often been confirmed in the literature (RYDEN 1983; LINN and DORAN 1984; WEIER et al. 1993; SHELTON et al. 2000). Also, GROFFMAN and TIEDJE (1988) used soil cores in a lab experiment to prove the promoting and inhibiting effect of wetting and drying cycles, respectively, on denitrification.

Gaseous N emissions did not occur above approx. 30 vol.% air, whose volume corresponds to 68 % water filled pore space (wfps) (Fig. 3). Nevertheless, such a threshold value was not uniform for all peat substrates but varied considerably (AGNER 2003). Also, it did not reflect air distribution within the substrate, as it is only a mean value of the substrate air content per pot. However, air content increased from the bottom to the surface of the pot. Consequently, the mean air filled pore space did not reflect oxygen availability at the potential sites of denitrification.

The sudden rise in denitrification N emissions at a distinct water level was often observed and various threshold values for water content increasing or limiting denitrification are reported in the literature. Values are often presented as wfps, as this unit was considered to make comparisons between soils of different texture easier (AULAKH et al. 1991; DE KLEIN and VAN LOGTESTIJN 1996). Nevertheless, values from the literature vary strongly and range from 62 to 90 % wfps (RYDEN 1983; AULAKH et al. 1991; WEIER et al. 1993; DE KLEIN and VAN LOGTESTIJN 1996; SHELTON et al. 2000). Thus, the observed value of 68 % wfps, or 30 vol.% air content of substrate, fits well into the reported range.

The dynamic nature of denitrification N emissions depending on aeration of the substrate was also underlined by the observation that increased transpiration resulted in an earlier termination of denitrification, since water content of the substrate dropped faster (Fig. 5). Thus, temporal variability of denitrification N loss between irrigation events could be attributed to variability of climate (vpd) (Fig. 6, which mainly controlled transpiration (Fig. 7). Nevertheless, more factors must have contributed to variability of N loss as even at uniform climate conditions high variability of N loss among pots was observed (Fig. 6).

Effect of plant age on denitrification

As transpiration was also affected by leaf area, the influence of plant age on N emissions was investigated

(Fig. 8). The older plants used for experiments had a nearly threefold higher shoot weight than the younger plants (data not shown). Consequently, transpiration was higher, substrate water content decreased faster and N emissions ended sooner with eight than with four week old plants. However, increasing plant age and size did not lead to a significant reduction of mean N loss per pot. While the duration of N emissions was shortened, emission rates of eight-week old potted plants increased sooner and reached a maximum, which was more than twice as high as those of four-week old potted plants (Fig. 8). Higher root mass of the older plants might have led to accelerated consumption of oxygen within the substrate and thus to a faster increase of N emissions relative to the younger plants. Additionally, respiration from a higher root mass might have caused increased availability of carbon.

In this experiment, stimulating and reducing plant effects on denitrification took place at the same time. In the literature, the promoting effect of plants on denitrification was attributed to oxygen consumption and rhizodeposition (SMITH and TIEDJE 1979; WOLLERSHEIM et al. 1987; PRADE and TROLLDENIER 1988; MAHMOOD et al. 1997). Limitation of denitrifying activity by plants was also observed, but it was ascribed to low nitrate availability in the rhizosphere due to nitrate uptake by plants (SMITH and TIEDJE 1979; RYDEN 1983). There is only little information on the influence of plant water uptake on denitrification. Possibly this is because most research has been carried out in agricultural soils where under field conditions the influence of plants on soil water dynamics is less obvious than in the present study.

From the data presented it may be concluded that potted plants exert a strong effect on the variability of denitrification N loss, mostly by controlling water and air dynamics in the substrate. Plant age and size within the same species did not contribute significantly to variability of N loss as reducing effects were apparently compensated for by stimulating effects on denitrification.

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