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Chapter 3

NITROUS OXIDE EMISSIONS FROM TERRESTRIAL PLANTS: OBSERVATIONS, MECHANISMS AND IMPLICATIONS

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ABSTRACT

This chapter reviews recent research on nitrous oxide (N_2O) emissions from terrestrial plants. This source of N_2O has been greatly ignored in most previous N_2O flux measurements in terrestrial ecosystems, and may cause errors in the estimate of N_2O fluxes from some terrestrial ecosystems. The contribution of N_2O emissions from such terrestrial ecosystems to the inventory of atmospheric N_2O is likely underestimated. Nitrous oxide emissions from terrestrial plants could be a major "missing" source of global N_2O budget. This chapter reviews up-to-date information on N_2O emissions from plants. It covers early representative evidence of N_2O emissions from plants, the mechanisms of N_2O production in plants as well as transport through plants. The chapter also reviews likely major controlling factors governing N_2O emissions from plants, and presents a conceptual model to integrate the available information. At the end of the chapter, information on the exchange of other N trace gases between plants and the atmosphere is briefly reviewed, and the implication of N_2O emissions from plants on global N_2O budget is discussed.

1. INTRODUCTION

Research interest on N_2O mainly comes from its two environmental characteristics: (1) an important atmospheric trace gas contributing to the enhanced global greenhouse effect, and (2) a natural catalyst responsible for ozone destruction in the stratosphere (IPCC, 2001).

Major biological sources of N_2O are microbial nitrification and denitrification processes. The nitrous oxide molecule is very stable in the troposphere, and photolysis in the stratosphere is the most important consumption mechanism. The only known biological mechanism of N_2O consumption is the last step of denitrification where N_2O can be reduced to nitrogen gas (N_2).

Nitrous oxide concentrations in the troposphere have been continuously increasing by 0.2 to 0.3% annually. In spite of the extensive efforts undertaken to identify the global N_2O dynamics from different sectors, there are still many uncertainties. Recent reports from the Intergovernmental Panel on Climate Change (IPCC) concluded that the global budget of N_2O is in better balance than previous reports, but uncertainties in the emissions from individual sources are still quite large.

The primary driver for the industrial era increase of N_2O was due to enhanced microbial production in expanding and fertilized agricultural lands (IPCC, 2001 and 2007). Understanding the importance of N_2O emissions from plants may help to better quantify the sources of N_2O from soil-plant ecosystems.

2. OBSERVATIONS

More and more reports are available on N_2O emissions from terrestrial plants. Interest in this research mainly comes for two reasons, understanding the physiological mechanisms of N metabolism in plants and an additional source of atmospheric N_2O with significance in global climate. Here we introduce only two representative case studies from the authors' research group.

2.1. N_2O Emission from Bacteria-Free Plant Samples

Nitrous oxide production has long been recognized as an intermediate product of microbial activities responsible for soil N transformation, namely nitrification and denitrification process. Nitrogen transformation also occurs during plant N metabolism, mainly for synthesis of protein by assimilating N nutrients. To test the hypothesis that plants may also emit N_2O during N metabolism, bacteria-free plant samples were used in an early study (Huang et al., 1992).

In this study, soybean seedlings were cultivated aseptically in the laboratory for 30 days. Hoagland culture medium with 200 mg nitrate-N L^{-1} was used. Intact seedlings, as well as different parts of the soybean seedlings, were enclosed in an air-tight glass bottle. The results showed detectable N_2O emissions from such bacteria-free plant samples (Table 1). The N_2O emission rates varied for different parts of the plant, in an order of leaf > cotyledon > stem. This study excluded any microbial contribution (such as from microbial nitrification and denitrification) to the detected N_2O emissions, and thus provided a direct evidence that plants can emit N_2O by themselves. Results from similar bacteria-free plant samples are also summarized in Table 1.

Table 1. N_2O emissions from bacteria-free plants

Plant species	N_2O emission rate	Reference
Soybean seedings	μg N_2O g^{-1}fw d^{-1}	Huang et al., 1992
Leaf	4.3	
Cotyledon	2.5	
Stem	0.1	
Intact plant	1.5	
Intact plants	μg N_2O g^{-1}dw d^{-1}	Li and Chen, 1993
Soybean	20.2 (6.0 to 73.9)	
Spring wheat	14.7 (0.24 to 32.6)	
Millet	6.6 (1.4 to 16.3)	
Wheat seedlings	pmol N_2O m^{-2} s^{-1}	Smart and Bloom, 2001
Leaf	25.36 ± 1.7	

2.2. Vertical Profile of Ambient N_2O Concentrations in a Natural Forest

Nitrous oxide emissions from terrestrial plants may be a common phenomenon. It was hypothesized that a significant amount of N_2O might be released from foliage of plants in forest ecosystems, which is normally ignored in N_2O flux measurements.

To test such a hypothesis, vertical profiles of ambient N_2O concentrations were measured several times in a natural forest (Xu et al., 2001). The study site was a coniferous and deciduous mixed forest located in the Changbai Mountain Biosphere Reserve, China (42°24'N, 128 °28'E).

The forest stand was a 290-year-old primary forest with an average canopy height of 28 m (canopy's upper and lower boundary approximately 31 m and 7 m, respectively, above ground). Ambient air samples were taken synchronously at 14 different heights of a 61.5-m research tower in the forest.

The results showed that the background atmospheric N_2O concentrations, represented by the measurements at the 61.5 m above ground, were quite constant (mean = 0.31, SD = 0.003 μLL^{-1}, n = 4).

However, vertical profile analysis showed that ambient N_2O concentrations reached maxima at or near the forest canopy height, suggesting N_2O emissions from the forest foliage. Occasionally, the maximum N_2O concentration along the vertical profile was > 60% higher than the background atmospheric levels (Figure 2). Similar results were also found, using a 5-m tower, at an 11-year-old secondary forest with an average canopy height of 3.2 m. The vertical profiles (at 8 different heights) of the ambient N_2O concentrations showed that the highest N_2O concentrations appeared right above the upper boundary of the canopy (Xu et al., 2001).

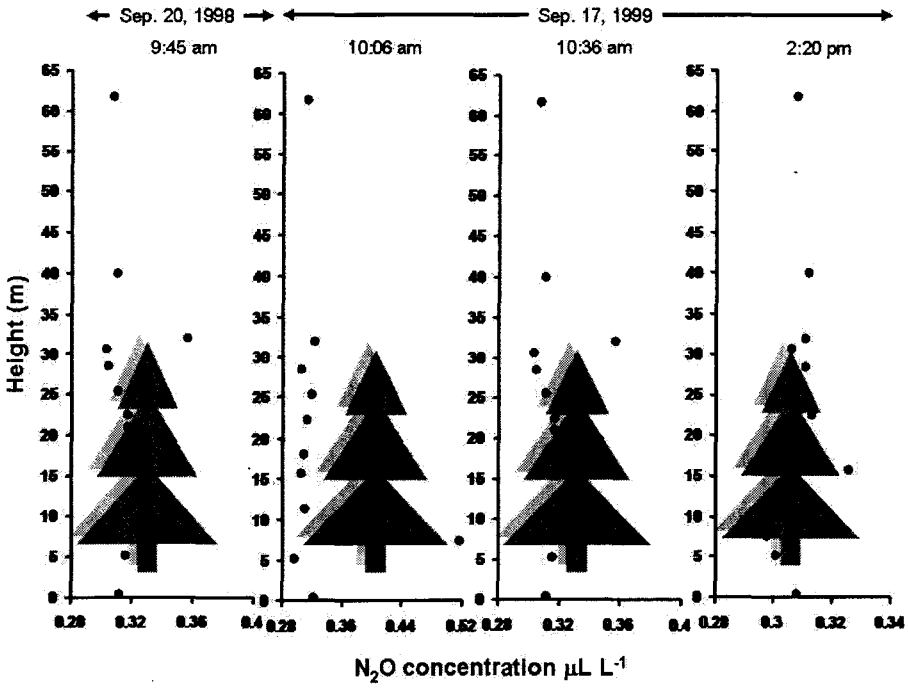

Figure 2. Vertical profiles of the ambient N_2O concentrations in a coniferous and deciduous mixed forest (modified from Figure 3 in Xu et al., 2001).

The observed elevated N_2O concentrations at/near the forest canopy indicated an outward flux of N_2O from the forest foliage to the atmosphere. This ambient N_2O concentration profiles can not be interpreted by N_2O emissions from the forest soil surface, because in that case N_2O concentrations would show a continuous decreasing trend from the forest floor to the top of the tower under stable meteorological conditions. This study suggests that plants could be an important source of atmospheric N_2O in a forest ecosystem.

3. MECHANISMS

3.1. Transport of N_2O by Plants

In terrestrial ecosystems, soil microbial nitrification and denitrification processes are the major sources of N_2O production. Nitrous oxide is highly soluble in water, and both soil solution and soil air have been found to be super-saturated with N_2O (Figure 3). Soil N_2O concentrations have been commonly found to be 1 to 3 orders of magnitude higher than the atmospheric levels. Despite the large variations observed in each system, fertilized agricultural ecosystems generally showed higher concentrations of soil N_2O than unfertilized natural systems. Nitrous oxide emissions from soil surfaces are driven by the large gradient of N_2O concentrations between soils and the atmosphere. The most important mechanism of N_2O emission from soils is molecular diffusion. Mass flow of N_2O by convection is less significant, but can be triggered by rapid changes in pressure, temperature, and water table (Heincke and Kaupenjohann, 1999).

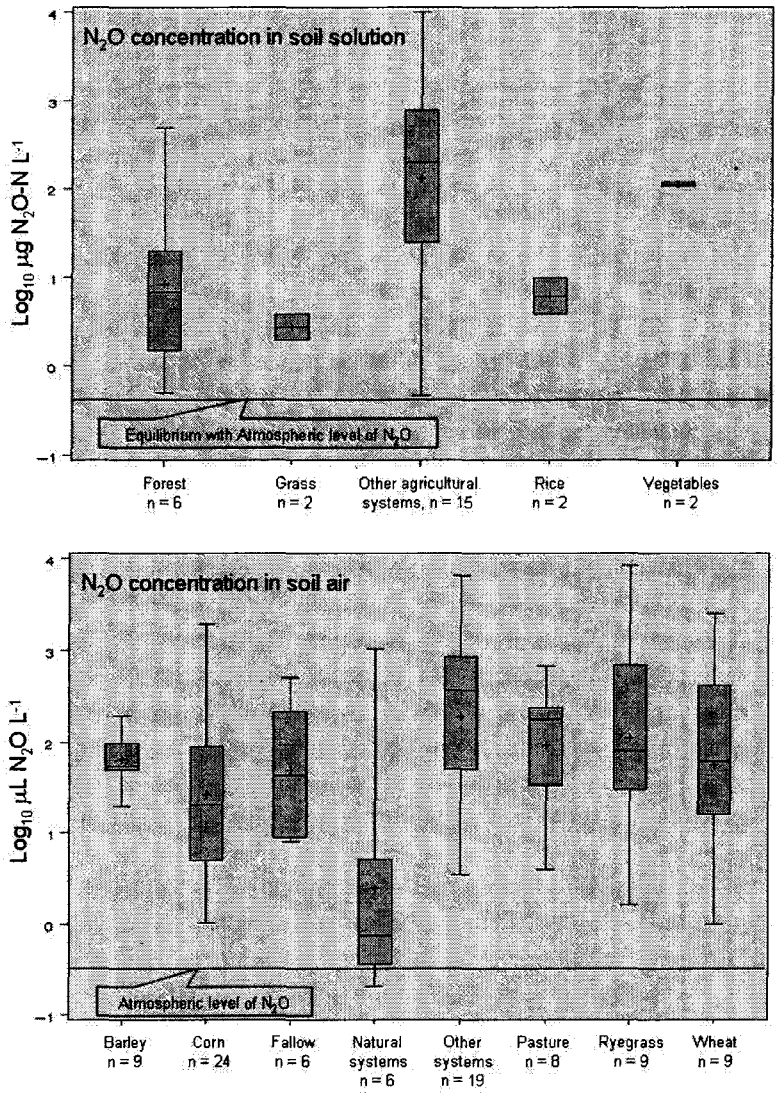

Figure 3. N_2O concentrations in soil solution (top) and soil air (bottom) (modified from Table 1 and 2 in Heincke and Kaupenjohann, 1999). Data are presented in Box-and-Whisker plots where statistical details are shown, 10th percentile (lower error bar), 25th percentile (bottom edge of the box), means (interior cross), median (interior horizontal line), 75th percentile (upper edge of the box), and 90th percentile (upper error bar).

Transport of soil N_2O to the atmosphere by terrestrial plants occurs through two major pathways: (1) N_2O transport in gas phase through plant pore spaces (aerenchyma) mainly found in wetland species and (2) N_2O transport in liquid phase through plant fluid systems, especially through the transpiration process in non-aerenchymous species.

Gas transport through the aerenchyma system in wetland plants is well documented, especially in rice systems. As a morphological adaptation to flooding conditions, wetland plants develop such pore spaces to allow influx of O_2 through plants for root respiration (Justin and Armstrong, 1987; Perata and Alpi, 1993). The same pathway is also used for efflux of soil gases in the opposite direction to the atmosphere. The studied gases include:

CH_4 (Schimel, 1995; Yu et al., 1997b), N_2O and N_2 (Mosier et al., 1990; Yu et al., 1997b), H_2 (Schütz et al., 1988), CO (Conrad et al., 1988), and CO_2 (Thomas et al., 1996).

As found in herbaceous wetland plants, such as rice (*Oryza sativa* L.), aerenchyma formation in response to flooding condition has also been found in other wetland tree species, including *Cyperus papyrus* L. (Li and Jones, 1995), *Alnus japonica* (Yamamoto et al., 1995a), *Fraxinus mandshurica* Rupr. *var. japonica* Maxim. (Yamamoto et al., 1995b), *Taxodium distichum* (L.) Rich. *var. distichum* (Kludze et al., 1994), *Alnus rubra* Bong. (Harrington, 1987), and even flood-tolerant *Pinus spec.* (Topa and McLeod, 1986). These woody species can serve as potential conduits for transporting trace gases produced in soils to the atmosphere. Rusch and Rennenberg (1998) found that black alder (*Alnus glutinosa*), a wetland tree species, emitted N_2O through the bark of the tree when N_2O concentrations in the soil solutions were higher than the atmospheric N_2O concentration. Gas efflux rates decreased with increasing stem height and correlated with the gas mixing ratios in the soil, indicating diffusion through the aerenchyma as a major path of gas transport.

Recent studies suggest that significant amounts of N_2O may be released to the atmosphere by plants through the transpiration process. Upland plants without aerenchyma system were used for this investigation to avoid N_2O transport by gas diffusion. Laboratory studies with similar approaches were conducted using barley (*Hordeum vulgare*), canola (*Brassica napus*) plants (Chang et al., 1998), and beech seedlings (Pihlatie et al., 2005). All of these studies reached the same results that exposing the plant roots to soil solutions with elevated concentrations of N_2O caused an immediate release of N_2O from the plant foliages. As a water-soluble gas, N_2O can theoretically be taken up by roots of the upland plants and be transported to the leaves via the transpiration stream. Since plant transpiration is a universal process, N_2O emission through the transpiration stream may be a common phenomenon for all plants.

The rates of N_2O emission by this plant transpiration-mediated mechanism will largely depend on the concentration of N_2O in soil solutions. As summarized in Figure 3, N_2O has been commonly found to be super-saturated in soil solution and soil air. Under favorable conditions for N_2O productions, generally characterized by moderate soil moisture content and relatively low gas diffusion rate, plant transpiration could play a significant role in transporting soil-derived N_2O to the atmosphere. Stomata represent the main pathway for gas exchange by non-aerenchymous plants. Meteorological (such as moisture, temperature) and plant physiological factors regulating stomata conductance will also affect the N_2O emission rates from plants.

3.2. Production of N_2O by Plants

It has long been hypothesized that plants may produce N_2O during N assimilation processes, since N transformation occurs for plant metabolism (Pate, 1973). Nitrate, taken up by plant roots from soil solution and relocated throughout the plant, must be reduced to ammonium form before it can be assimilated into amino acids and proteins. Like the soil microbial denitrification process, there is evidence that higher plants also have denitrifying abilities where nitrate and nitrite can be reduced to N gases (Dean and Harper, 1986; Harper, 1981). For example, it has been reported that detached wheat leaves could assimilate nitrite and release it as N_2 (Vanecko and Varner, 1955). Nitrite assimilation in soybean chloroplasts

can generate intermediates capable of reacting to produce N_2O (Dean and Harper, 1986). It is generally believed that any enzymatic N transformation through the +2 to +1 oxidation state may generate N_2O (Firestone and Davidson, 1989).

Using bacteria-free or near bacteria-free plant samples, several earlier studies reported N_2O emissions by crops, such as soybean, wheat, and maize (Harper, 1981; Chen et al., 1990; Huang et al., 1992; Li and Chen, 1993; Smart and Bloom, 2001). Using ^{15}N-labelled nitrate as a tracer, Hakata et al. (2003) provided more direct evidence of N_2O emission by plants, instead of by any microbial activities. Cross culture experimental design was applied in their study with 17 plant taxa that had been cultured aseptically. At the beginning of the experiment, the plants were cultured in ^{15}N-labelled nitrate medium for one week (feeding period). Then the plants were transferred to a medium with non-labeled nitrate and cultured for another week (emission period). The amount of labeled N_2O emitted from the plants during the emission period was determined. The results found that all tested plants, with one exception, showed emissions of ^{15}N-labeled N_2O. The N_2O emission rates largely varied among the plants, but reflected only a small portion of the capability of plants to convert nitrate to N_2O. It was concluded that converting nitrate to N_2O must be common in plants.

Smart and Bloom (2001) also found that N_2O could be formed by enzyme activities inside plant leaves. It was first found that the N_2O emission rate from wheat leaves was increased by more than 10 times when the N source was shifted from ammonium to nitrate. It was recognized that leaf N_2O emissions were mainly correlated with leaf nitrate assimilation activity. Production of N_2O in vitro was found associated with both intact chloroplasts and the nitrite reductase, but not with the nitrate reductase, indicating that N_2O produced by leaves occurred during photo-assimilation of nitrite in the chloroplast. It was concluded that the two enzymes responsible for plant nitrate assimilation, nitrate reductase and nitrite reductase, are located in the cytoplasm and chloroplasts, respectively. The study provided in vitro evidence that the N_2O emitted from the wheat leaves was generated by nitrite reduction (N oxidation state +3) to ammonium (N oxidation state -3) in the chloroplasts, with N_2O (N oxidation state +1) emission as an intermediate product.

Two herbicide-treated soybean plants were used for studying N_2O emissions from such plants (Zhang et al., 2000). It has been previously found that the two herbicides used in this study, Bromoxynil a photosynthetic inhibitor and 2, 4-D a non-photosynthetic inhibitor, can cause nitrite accumulation in plant tissue (Klepper, 1979). The study showed that nitrite concentrations in the herbicide-treated soybean plants were about 5 times higher than in the control plants, while nitrate concentrations remained the same. Meanwhile, N_2O emissions from the herbicide-treated soybean plants were about twice as much as from the control plants. Nitrite is generally toxic to most biological organisms. It is believed that accumulation of nitrite during nitrate assimilation is the major cause for N_2O production and release, by which toxic nitrite is removed. Using transgenic tobacco plants, Goshima et al (1999) reached the same conclusion. The nitrite reductase activity in the transgenic tobacco plant was suppressed to less than 5% of the wild type plant. Nitrite content in such transgenic plants grown on nitrate-containing medium has been reported to be about 5 times higher that in wild-type plants (Vaucheret et al., 1992). All plants were cultured aseptically with no involvement of microbes. No N_2O emission was found from the transgenic or wild-type plants grown on ammonium-containing medium. Immediate emissions of N_2O were found when the plants were fed with ^{15}N-labeled nitrate or nitrite. Nitrous oxide emissions from the tobacco plants could be inhibited by applying tungstate (a nitrate reductase inhibitor). Nitrous

oxide emission from the wild-type tobacco plants grown on 2mM ^{15}N-labeled nitrite-containing medium was also detectable. However, the quantity of ^{15}N-labeled N_2O emitted from the wild-type grown on the nitrite medium was only about 7% from the transgenic plants. It was also found that emission rates of N_2O from the transgenic plants increased with increasing nitrite levels in the plants. These findings indicate that nitrite is a precursor for N_2O formation in plants and that N_2O is not derived from ammonium or its derived metabolites. It is interesting to see that in this study no N_2 emission was found from both the transgenic and wild-type plants grown on ^{15}N-labeled nitrate-containing medium. The result is in contrast to the microbial denitrification process where N_2 is commonly the dominant product.

Given the large quantities of nitrate assimilated by plants in the terrestrial biosphere, it is suggested that N_2O emission during nitrite photo-assimilation could be an important biogenic N_2O source with global significance. According to Smart and Bloom (2001), this enzymatic production of N_2O in the leaves could account for 5–6% of the total N_2O emissions from agricultural soil–plant systems.

3.3. Controlling Factors for N_2O Emissions from Plants

Nitrous oxide emission rates from plants are likely related to plant species, different plant parts and growing stages, nutrients and light conditions to the plants. Information on these regulating factors is summarized as follows.

(1) N_2O emissions from different plant species

Measurements of N_2O emission from plants have been conducted using various plant samples, ranging from wetland plants to upland species, and from agricultural crops to woody plants. Table 2 summarizes the reported N_2O emissions from naturally growing plants. Most of them are from non-aerenchymous species, except one wetland species, black alder. All the measurements were conducted in near bacteria-free conditions in the laboratory or in the field conditions. It seems that N_2O emissions from plants are widely existing phenomena. However, when using intact plants, it can not distinguish if the source of N_2O is from inside the plant, or from transportation of soil N_2O through the plant transpiration stream.

(2) N_2O emissions from different parts and different growing stages of plants

As already known, nitrate reductase and nitrite reductase, the two enzymes responsible for plant nitrate assimilation, are located in the cytoplasm and chloroplasts, respectively. Nitrous oxide production and emission is likely more significant in plant organs with active metabolism. Nitrous oxide emission rates were found different from different parts of the soybean plant. The highest N_2O emission rate was found from the soybean leaves where photosynthesis and N assimilation are the most active (Table 1). Seasonal analysis of N_2O emissions from intact soybean, wheat and millet showed that N_2O emission rates were lowest in early vegetative growth stage, and highest in flowering and reproductive stage (Li and Chen, 1993). It clearly indicates that N_2O emissions from plants are strongly associated with plant N metabolism at different physiological status.

Table 2. N_2O emissions from different plant species

Plant species	N_2O emission rate	Reference
Tree leaves	μg N m^{-2} h^{-1}	Yang et al., 1995
Abies hollophylla	1.7	
Alnus hirsuta	1.2	
Larch	81.3	
Korean pine	12.5	
Poplar	74.3	
Crop seedlings	μg N kg^{-1}dw h^{-1}	Chen et al., 1995
Maize	66	
Soybean	45	
Sorghum	59	
Tree barks	μmol N_2O m^{-2} h^{-1}	Rusch and Rennenberg, 1998
Black alder	350	
(Alnus Glutinosa)		
Tree branches	μg N kg^{-1}dw h^{-1}	Zhang et al., 2002
Fraxinus mandshurica	22.9 (6.0 to 97.3)	
Pinus koraiensis	14.8 (0.1 to 41.1)	
Alnus hirsuta	16.3 (-7.7 to 41.2)	
Tilia amurensis	0.02 (-7.1 to 10.2)	
Tree seedlings	μg N m^{-2} h^{-1}	Pihlatie et al., 2005
Beech (Fagus sylratica)	0.4	
Intact crop	μg N kg^{-1}dw h^{-1}	Zou et al., 2005
Winter wheat	75 to 394	

(3) Effect of nutrients on N_2O emissions from plants

Plants generally prefer ammonium instead of nitrate for growth. Assimilation of ammonium into amino acids is a more energy efficient pathway for plants. In contrast, assimilatory reduction of nitrate to ammonium is an energy consuming process, where N is reduced from oxidation state +5 to -3. Research by Pate (1973) showed that presence of a low level of ammonium in the medium has only a slight inhibitory effect on the uptake of nitrate, but it expresses a much higher restriction on the amount of nitrate incorporated into organic compounds. When plant roots received both ammonium and nitrate, much lower level of nitrate reductase was found in the roots, suggesting that ammonium can inhibit the synthesis of nitrate reductase.

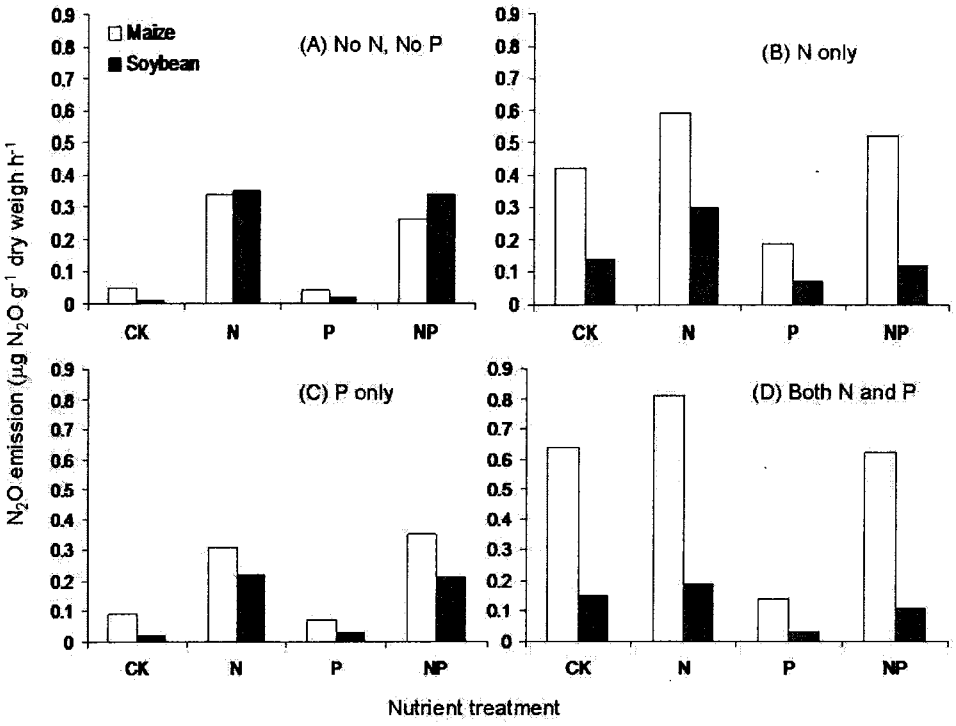

Figure 4. Effect of nitrate-N and phosphate-P on N_2O emissions from maize and soybean seedlings in aquatic culture. Samples were previously aseptically cultured in sand with different nutrient treatments: (A) No N and no P, (B) N only, (C) P only, and (D) Both N and P (Modified from Table 2 in Chen et al., 1997b).

Expression of nitrate reductase genes is light-dependent, following a diurnal pattern. Nitrate reductase is also nitrate-inducible when nitrate in the system exceeds certain limit (Hoff et al., 1994). Results of xylem sap analysis showed a good correlation with the pattern of distribution of nitrate reductase and storage of excess N in plants (Pate, 1973). Part of the accumulated nitrate in plants may go to the assimilatory reduction pathway for synthesis of amino acids, and the other may go to dissimilatory reduction pathway with N_2O as a byproduct.

Accumulation of nitrite in plants is probably a good indicator of occurrence of dissimilatory nitrate reduction. Nitrite reductase is directly responsible for N_2O production, by which highly toxic nitrite can be quickly removed from the plants.

Almost all N fertilization (no matter of ammonium or nitrate fertilizers) studies showed stimulation of N_2O emission from plants (Li and Chen, 1993; Figure 4). Presence of ammonium will inhibit the assimilation of nitrate, but not the uptake of nitrate by plants, likely resulting in nitrate accumulation in plants. Most of the studies showed a good correlation between N_2O emission rates from plants and nitrate contents as well as nitrate reduction activity in plants.

Fertilization is essential to maintain proper plant growth and productivity. It is important to keep nutrients in balance to meet the plant needs at different growth stages. Otherwise, imbalanced nutrition may cause N in relative excess, which may subsequently result in enhanced N_2O emissions from plants. By using a cross-culture method, Chen et al. (1997b)

studied N_2O emissions under different combinations of N and P supplies (Figure 4). The results clearly showed that applying N caused significant increase in N_2O emissions from the maize and soybean plant. Meanwhile, applying P could substantially reduce N_2O emissions from the plants, even lower than from the non-fertilized control plants. Changes of nutritional status could immediately alter the N_2O emission rates from plants, as seen in this study where the plants were transferred from sand culture to aquatic culture of different N and P combinations. It can be expected that other essential nutrients for plant metabolism, such as potassium (K), may play a similar role as P in this study to regulate the nutrient balance in plants and N_2O emission rates from the plants.

(4) Effect of light conditions on N_2O emissions from plants

It is well known that light energy is ultimately involved in the assimilation of nitrate in plants. It is likely that N_2O emissions from plants are strongly associated with plant photosynthesis activity.

During an in vivo nitrate reductase assay, it was found that light treatment resulted in much less nitrite accumulation compared with the normal dark assay (Harper, 1981). Aslam et al. (1979) examined the influence of light, dark, and ambient CO_2 on nitrate assimilation in barley seedlings.

The seedlings were first grown in N-free Hoagland solution for 5 days in darkness followed by 3 days in continuous light. The results showed that the seedlings could reduce nitrate and nitrite in both light and dark conditions. Nitrate reduction in the darkness was relatively slow, but nitrate uptake was not decreased, resulting in a doubled internal concentration of nitrate.

The faster nitrate reduction in the light treatment was attributed to recent photosynthetic products, supplying energy for the reactions possibly by shuttle reactions between chloroplasts and cytoplasm. In carbohydrate-deficient tissue, it appeared that recently fixed photosynthetic products could supply all the energy required for nitrate reduction. Meanwhile, photosynthetic products also served as substrates for synthesis of other organic compounds in connection with N assimilation.

Chen et al. (1997a) simultaneously studied photosynthesis and N_2O emissions from two N-fixation plants. They found that both light and ambient CO_2 concentrations significantly affect N_2O emissions from the plants (Table 3).

As expected, photosynthesis activity in the plants increased with increase of light intensity and CO_2 concentrations. Nitrous oxide emissions from the plants showed the opposite trends, with low N_2O emissions, even uptake of ambient N_2O, found under strong light and high CO_2 concentration conditions.

The results provided clear evidence of a close linkage between N_2O emissions from plants and plant photosynthesis activity. Higher N_2O emissions from plants likely occurred under unfavorable conditions for plant photosynthesis, such as weak light and low CO_2 concentrations. It can be expected that certain climatic conditions, such as water stress due to drought, also affect plant photosynthesis activity and N_2O emissions from plants as a consequence.

Table 3. Photosynthesis and N_2O emissions from two N-fixation plants, soybean and hippophae (Modified from Table 4 in Chen et al., 1997a)

	Light (lx)	CO_2 concentration ($\mu L\ L^{-1}$)					
		360		465		600	
		Soybean	Hippophae	Soybean	Hippophae	Soybean	Hippophae
Photosynthesis ($mg\ CO_2\ dm^{-2}\ h^{-1}$)	0	-1.6	2.1	-0.7	-1.9	-0.4	0.4
	3000	1.6	0.6	2.6	1.4	4.3	2.1
	10000	5.2	2.3	7.9	3.1	12.8	3.7
	30000	7.2	6.4	11.4	12.5	15.9	12.5
N_2O emission ($ng\ N_2O\ dm^{-2}\ h^{-1}$)	0	5.9	-9.5	-11.8	-16.9	-4.2	-0.2
	3000	24.5	-14.0	0.1	-18.6	-3.8	-4.1
	10000	15.1	-10.9	13.8	-23.4	12.9	-2.0
	30000	-7.7	-11.8	-17.3	-19.3	-4.6	-2.5

Both N_2O emission and absorption by plants were observed in this study (Table 3), which indicated that N_2O emission from plants is a dynamic process as a net result of production and consumption. Lensi and Chalamet (1981) also found that plant leaves are able to absorb N_2O. There must be a N_2O compensation point, where N_2O production equals its consumption at a certain condition, with no net flux of N_2O between plants and atmosphere. When N_2O production exceeds its compensation point, N_2O emissions from plants occur. On the other hand, when N_2O consumption exceeds its compensation point, N_2O absorption by plants occur.

3.4. Conceptual Model of N_2O Production in Plants

The concept of N_2O compensation point is critical to understand the dynamic processes of N_2O in plants. Any factors that can alter N_2O production and consumption in plants will ultimately determine whether the plant is a source or a sink of atmospheric N_2O, as well as the strength of the source or sink. To our knowledge, there is little information on the mechanisms of N_2O consumption in plants. As a summary to what we know on the factors governing N_2O production in terrestrial plants, we present a conceptual model consisting of both photosynthesis and N assimilation pathways (Figure 5). Major factors regulating N_2O production in plants are integrated into the model. Energy (ATP) and reductants (NADH and

NADPH) required to assimilate N may be provided by photosynthesis, respiration or both (Turpin et al., 1997).

Production of N_2O in plants is strongly associated with the balance between photosynthesis and inorganic N assimilation processes. Nitrite reductase, mainly responsible for N_2O production in plants, is located in chloroplast, indicating a strong linkage between photosynthesis and N metabolism. For example, Smart and Bloom (2001) reported that wheat leaf N_2O emissions were correlated with leaf nitrate assimilation activity, as measured by the assimilation quotient (the ratio of CO_2 assimilated to O_2 evolved). Assimilation of inorganic N requires C skeletons that are provided by photosynthesis (new C) and respiration (stored C). Although our understandings on the regulatory mechanisms of N_2O production in plants are still preliminary, it is certain that both N and C flow in plants are involved.

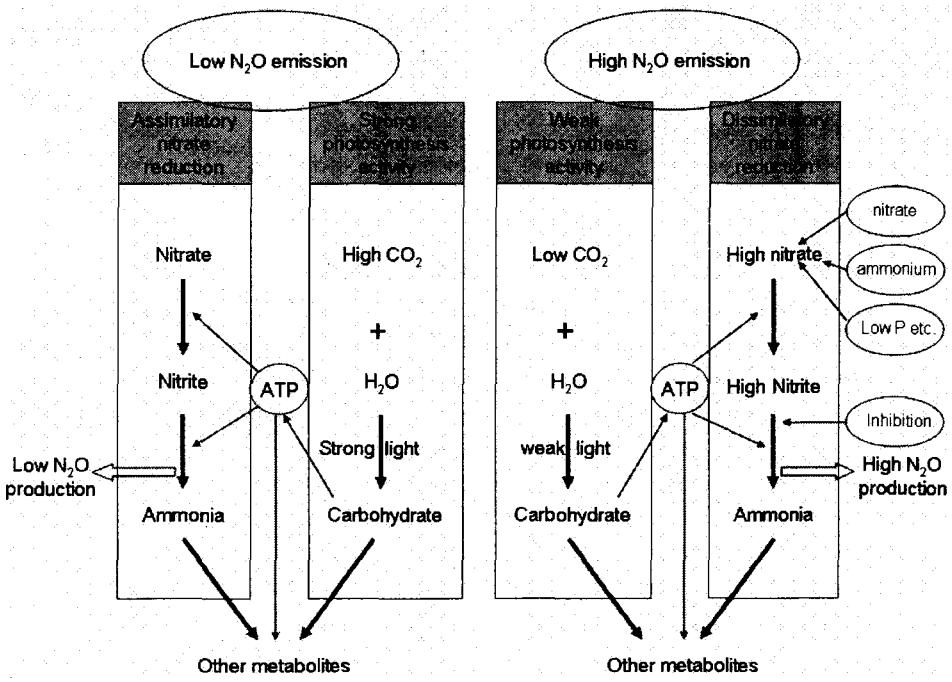

Figure 5. Conceptual model of important factors regulating N_2O emissions from plants.

This conceptual model can explain most of the reported findings on N_2O emissions from plants. Lower N_2O emissions from plants occur when plant photosynthesis activity is significant supported by higher ambient CO_2 concentration and strong light, and nitrate is mainly in assimilatory reduction pathway. Dissimilatory nitrate reduction process is responsible for N_2O production in plants, which can be controlled by (1) weak photosynthesis in plants due to lower ambient CO_2 concentrations and weak light, and/or (2) excess nitrate and nitrite in plants due to imbalanced nutrient supplies or certain inhibitors of nitrite reduction.

It is important to know that both assimilatory and dissimilatory nitrate reduction exist in plants at the same time. In many cases, stored C and N in plants play some roles in the observed results through internal cycling processes. Future studies are strongly needed to modify this model and elucidate the observed results.

4. OTHER NITROGEN GASES

Long before the observations of N_2O emissions from higher plants, exchange of other N trace gases between plants and the atmosphere have been studied. Most important and well-studied N gases include nitric oxide (NO), nitrogen dioxide (NO_2), and ammonia (NH_3). With other nitrogenous oxides, NO and NO_2 are commonly referred as $NO_{(x)}$. It is important to know that productions of these N trace gases commonly occur simultaneously in plants. An in vivo nitrate reductase assay showed that the predominant N gas evolved from soybean leaves is NO with trace amounts of N_2O and NO_2 (Dean and Harper, 1986). An in vitro study showed that NO generating capacity could only account for less than 1% of the total nitrate reductase activity, indicating production of N gases is only a small part of the N metabolism in plants (Rockel et al., 2002).

Exchange of many trace gases between plants and the atmosphere is bidirectional, including both emission and absorption. Factors regulating the compensation points of these N gases are interrelated. Studies on the mechanisms and controls of other N trace gases will greatly improve our understanding of N_2O emissions from plants. Future investigations on N_2O emissions from plants should integrate with other gaseous N species.

4.1. Emissions of Other Nitrogen Gases from Plants

Several early studies reported production of N_2, NO and N_2O when green leaf tissue or plant metabolites were treated with nitrite (Porter, 1969). Nitric oxide is probably the most studied N trace gas, and has been reported to be emitted by various higher plants such as sunflower, tobacco, maize, soybean, spruce, sugar cane, rape and spinach. The emission of NO by plants on a global scale is estimated to be in a range of 2.3×10^{11} g N per year (Wildt et al., 1997). Recently NO was shown to be a key signaling molecule in plants (Neill et al., 2003). Short-term heat stress caused an increase in NO production in alfalfa (Leshem, 2001). Application of NO mediates chilling resistance in tomato, wheat and maize (Lamattina et al., 2001). The mechanism of NO production in plants is still subject to future investigation, but it seems similar to that of N_2O production. Nitrite clearly serves as a precursor of NO in plants, and NO production can be significantly increased in the dark. In this way, nitrite can serve as a mobile source of NO in plants. Typically, NO rapidly reacts with O_2 to form NO_2, which explains the co-occurrence of these two gases. Ammonia emission from plant's foliage has been demonstrated in studies, using soybean (Stutte et al., 1979) and barley (Mattsson and Schjoerring, 1996).

4.2. Absorption (Uptake) of Other Nitrogen Gases by Plants

The absorption of gaseous atmospheric ammonia by plant leaves is well documented (Hutchinson et al., 1972; Porter et al., 1972). Lockyer and Whitehead (1986) observed that ammonia absorption could account for 10-20% of the total plant N. Uptake of NO_2 by plants through the stomata was observed, and the NO_2 was assimilated into organic forms (Yoneyama and Sasakawa, 1979). In a maize field study, it was estimated that the amount of

NO_2 uptake by the maize canopy was as much as 27% of the soil-emitted $NO_{(x)}$ (Hereid and Monson, 2001). This kind of gaseous N source may play a critical role in the primary production in N-limited natural ecosystems.

There are evidences that NO_2 assimilation is related to the activities of nitrate and nitrite reductase in the plant leaves (Thoene et al., 1991). To study the uptake mechanisms by maize leaves, ^{15}N labeled NH_3 and N_2O were used. The results indicated two initial entry pathways for NH_3: (1) fast uptake with immediate metabolism, and (2) fast storage with progressive metabolism. A storage compartment delayed NH_3 absorption after exposure. Similar mechanisms might be involved in N_2O uptake (Grundmann et al., 1993).

5. IMPLICATIONS

5.1. Contribution of Plants on N_2O Emissions from Soil-Plant Systems

Nitrous oxide emissions from plants represent a previously overlooked pathway of N_2O emissions to the atmosphere from terrestrial ecosystems. The magnitude of this source of N_2O deserves further investigation.

Generally speaking, growing plants contribute to the N_2O emissions from a soil-plant system in three directions: (1) plant roots and root exudates facilitate microbial N_2O production in the soil, (2) plants can transport the soil N_2O to the atmosphere, and (3) plants can produce N_2O by themselves. The portion of N release as N_2O from the soil-plant system largely depend on the balance between N supply to the system and N incorporation into the plant production. Unfortunately, this balance is commonly distorted in agricultural ecosystems. It is a common practice for crop production to supply all fertilizer N at once or a few times in a growing season, which may sometimes cause the surplus N release as N_2O.

Nitrous oxide emissions from both a soybean field (using a static chamber to cover both the plant and soil) and the soybean plant (using a separate plant shoot chamber) were measured (Yu et al., 1997a). The seasonal analysis indicated that the soil and soybean plant contributed to 53% and 47%, respectively, of the total N_2O emissions. Using the combination of a conventional static chamber technique and a soil-surface sealed method, Chen et al. (2002) studied the contribution of soybean and maize plants to the overall N_2O emission from the two soil-plant systems. A complete seasonal measurement showed that N_2O emission from the plants accounted for 6-11% for the soybean and 8-16% for the maize, respectively, of the total soil–plant N_2O emissions. By cutting the above-ground part of the crop and in combination with the static chamber method, Zou et al. (2005) indirectly estimated the contribution of winter wheat in total N_2O emission from a soil-wheat system. The results show that the contribution of N_2O emissions from the wheat to the total N_2O fluxes from this system was 25% on average, ranging from 10% at tillering stage to 62% at heading stage. Similar cutting plant approach was used by Chen et al. (1999) in a rye grass (Lolium perenne L.) field. They found that total N_2O emission rates of the system varied between 0.8 and 13.3 mg N_2O-N m^{-2} d^{-1} with N_2O releasing from the rye grass plant between 0 and 2.8 mg N_2O-N m^{-2} d^{-1}. In a grassland study, Anderson and Hopkins (1997) found that *Linum perenne* contributed as much as 50% of the total N_2O flux to the atmosphere. Estimates from several forest ecosystems indicated that N_2O emissions from forest canopies are of the same order of

magnitude as soil-derived N_2O emissions from forest ecosystems in Europe (Ambus et al., 2001; Butterbach-Bahl et al., 2002) and in China (Zhang et al., 2002).

The above measurements and estimates could not distinguish the different mechanisms (transport by plants or production in plants) responsible for plant-mediated N_2O emissions. However, it is believed that N_2O transport through plants is a universal pathway. The magnitude of N_2O emissions from plants due to N_2O production in plants likely depends on the imbalance of N supply and demand for plant metabolism.

5.2. Balance the Global N_2O Budget

Synthesis of the available information on N_2O emissions from terrestrial plants strongly suggests that higher plants play an intriguing role in N_2O exchange between biosphere and atmosphere. Our current estimate of N_2O inventory from global terrestrial ecosystems probably deserves a careful revision. Most of the N_2O flux measurements in different terrestrial ecosystems are conducted using a static chamber technique (normally less than 1 m in height), covering a small area of land surface (normally less than 1 m^2). The N_2O emission rate from the covered area is calculated from the increase of N_2O concentration over time inside the chamber. Such small enclosures exclude tall plants and trees, and may consequently underestimate the N_2O emissions from certain soil–plant systems. In this case, micrometeorological techniques for gas flux measurement may be needed with the advantage of covering a larger area (0.1 to 1 km^2) of measurement, and not disturbing plant microclimate.

For grassland and agricultural ecosystems, plants are normally covered inside the static chamber for N_2O flux measurements, with some exceptions for tall grasses and crops (such as maize). There is some evidence showing that, despite the spatially and temporally heterogeneous conditions in fields, N_2O flux measurement using a small enclosure chamber technique is quite comparable to a field scale measurement using a micrometeorological technique (Hutchinson and Mosier, 1979; Christensen et al. 1996). However, Li et al. (2002) found that micrometeorological N_2O flux measurements over maize crop fields were several folds higher than those measured by the static chamber technique covering the soil only.

It is very likely that the N_2O inventory from global forest ecosystems is underestimated by using the static chamber technique covering a small area of the forest floor. Such enclosures exclude N_2O emissions from tall trees regardless of the different mechanisms involved, and therefore underestimate the N_2O flux from the whole ecosystem. It is worthwhile to mention that most of the information on N_2O emissions from forest trees is obtained from laboratory studies and using small tree seedlings. It was found that N_2O concentrations in beech leaves were much higher in laboratory seedlings than in forest trees, indicating that the natural N_2O emissions from plants may be much smaller than those measured in the laboratory (Pihlatie et al., 2005).

The global N_2O inventory shows large uncertainties in different sectors. Biogenic and anthropogenic sources of N_2O are poorly constrained. Recognition of N_2O emissions from plants may help to better quantify N_2O emission from soil-plant systems. Nitrous oxide flux measurements in soil-plant systems must consider the presence of plants by modifying existing techniques. Careful attentions should be paid for interpretation of the measurement results. Advancement in measurement techniques and estimation approaches will help to

quantify the spatial and temporal variations of N_2O emissions from field plot to ecosystem and global scale. Nitrous oxide emissions from terrestrial plants widely exist in natural environment, which might have implications in understanding the global N_2O budget before the industrialization era when the global N cycle was not severely altered by anthropogenic activities.

CONCLUSION

Recent studies on N_2O emissions from different terrestrial plants provide convincing evidence that plants are a potential source of atmospheric N_2O, which represents a net result of N_2O production and consumption in plants. This source of N_2O has long been ignored in the estimate of N_2O emissions from global terrestrial ecosystems, due to technical limitations of measurement and estimation. This direction of research represents an important advancement in recent N_2O research progress. Recognition of this source of N_2O will significantly improve our understanding of the global terrestrial sources of N_2O. The feedback of N_2O emissions from terrestrial plants on a rapid global climate change deserves future investigation.

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