Plant controls over tropical wetland nitrous oxide dynamics: a review

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Abstract

Tropical wetlands are an important global source of greenhouse gas emissions, including nitrous oxide, a potent and long-last greenhouse gas. Tropical wetland ecosystems can be highly heterogeneous, featuring a variety of vegetation types, from grasses through to palms and mangroves. A variety of plant-mediated processes can exert key controls over wetland plant/soil nitrogen transportation and transformations, including through litter inputs, rhizodeposition and root turnover regulating the size of the soil nitrogen pool, plant nitrogen uptake, rhizosphere biology, and plant-mediated nitrous oxide transportation all playing important roles, and in many cases varying between key wetland vegetation types. In this review, we summarise the importance of such processes in regulating tropical wetland nitrous oxide dynamics.

1. Introduction

Tropical wetlands are an important potential source of global greenhouse gas emissions, including carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), potentially accounting for as much as two-thirds of the latter at a global scale (D'Amelio et al., 2009). N_2O is a potent, long-lasting greenhouse gas (GHG), approximately 300 times more powerful at driving climate warming than CO_2 over 100 years and has caused 10% of total warming to date (Thompson et al., 2019). Concentrations have increased from 290 parts-per-billion (ppb) in 1940, to 330 ppb in 2017, and are rising annually by 0.3% (Thompson et al., 2019). Understanding the controls over N_2O dynamics is therefore essential in recognising the future impacts of environmental change on emissions (e.g. alterations in precipitation and soil warming), and to identify potential mitigation strategies.

Estimates of tropical and sub-tropical wetlands extent range from 1.4 - 4.7 million km^2 (Gumbricht et al. 2017). Tropical wetlands are highly heterogeneous in terms of vegetation, ranging from the largely undisturbed palm and broadleaved evergreen tree dominated peatlands of the Central Congo basin (Dargie et al., 2017), to Caribbean mangroves (Phillips et al., 1997), managed grasslands and woodlands of the Pantanal (Liengaard et al., 2014), to the extensively converted tropical peatlands of Southeast Asia (Cooper et al., 2020). This heterogeneity results in biogeochemical processes that can vary from the micro-scale (e.g. plant root aeration and exudation), meso-scale (e.g. plant type, and physiology), to the landscape scale (e.g. wetland ecotype and hydrology). The role of differences in vegetation in determining the production and emission of N_2O from tropical wetlands have thus far have been largely overlooked.

Understanding the role of plants in regulating emissions is important in several contexts: first, evidence suggests that under certain circumstances, for example, specific combinations of high nitrogen inputs and optimal water content, tropical wetlands of various types may be substantial but poorly quantified contributors to global N_2O budgets (D'Amelio et al., 2009). The importance of this is underlined by the limited flux measurements that have been made to date in globally important wetland systems, including the Pantanal (Liengaard et al., 2014), and intact and degraded Southeast Asian peatlands (Cooper et al., 2020). Second, although emissions (by mass) are lower than those of CO_2 and CH_4, N_2O has a substantially higher global warming potential, meaning that relatively small emissions will drive a disproportionate degree of warming (IPCC, 2021). Third, climate feedbacks, for example, the altering of precipitation patterns, and rising temperatures, may substantially alter plant productivity and inputs, and dominant vegetation types, altering N_2O production and emissions. Fourth, exploitation of the potential of tropical wetland restoration as a nature-based solution to climate change (Girkin & Davidson, 2024) will have implications for N_2O budgets through direct and indirect impacts on carbon and nitrogen flows.

Although many of the fundamental ecological and biogeochemical processes are similar, data from relatively well-studied temperate and boreal wetland systems cannot be readily applied to the tropics, due to substantial differences in plant species and plant functional types, ecosystem productivity, and climate (Sjögersten et al., 2014). This hampers the further development of process-based models that can accurately scale fluxes or test their sensitivity to future environmental perturbations (Farmer et al., 2011). Understanding the role of plants is therefore important to the task of identifying local and regional emissions hotspots, develop management practices that might mitigate emissions, and to understand potential impacts from global environmental change processes, including climate impacts and land use change that will affect dominant vegetation types (Girkin and Cooper, 2022). In this review, we assess the direct and indirect mechanisms by which plants and plant inputs may be regulating soil and sediment N_2O emissions. In so doing, we identify the dominant pathways and processes underpinning production to understand potential feedbacks from ongoing global environmental change processes and aim to highlight the critical need for better quantification of the scale of tropical wetland N_2O emissions.

2. Nitrous oxide emissions from tropical wetlands

Approximately two-thirds of biological nitrogen fixation occurs in tropical wetlands (Maltby and Barker, 2009). Nitrogen losses are predominantly driven by denitrification forming N_2O and/or atmospheric nitrogen (N_2) in a series of microbially-mediated processes. However, rates of nitrogen loss are generally much lower than inputs, making wetlands an important pool of nitrogen, with the majority stored in the organic pool in the microbial biomass, as recalcitrant organic matter, in macrophytes, and in plant litter (Reddy and DeLaune, 2008). Key environmental controls over wetland soil and sediment nitrogen cycling have been elucidated, and range from soil moisture, temperature, and pH (Butterbach-Bahl et al., 2013).

Microbial processes drive approximately 90% of global N_2O emissions (Butterbach-Bahl et al., 2013). Nitrification, the sequential oxidation of ammonium (NH_4^+) to nitrite (NO_2^-) and nitrate (NO_3^-), and denitrification, the reduction of NO_3^- to N_2O and dinitrogen (N_2), are recognised as the dominant processes in wetland soil nitrogen dynamics (Reddy and DeLaune, 2008). While the balance of these processes is determined by substrate supply, oxygen availability, moisture, and pH, both processes can occur simultaneously in soil microsites due to differences in oxygen availability. Nitrifiers can release N_2O at low oxygen availability when moisture content is equivalent to 60% water filled pore space (WFPS) (**Figure 1**) (Bateman and Baggs, 2005). Similarly, denitrifiers preferentially produce N_2O under low oxygen conditions. The proportion of N_2O as the end of product of denitrification increases at lower pH and may thus represent the dminant gaseous nitrogen production pathway in tropical wetlands (Reddy and DeLaune, 2008). Other processes may also contribute to emissions, but the balance of pathways is largely unknown. For example, in tropical peatlands, dissimilatory nitrate reduction can occur under NO_3^- limiting conditions (Espenberg et al., 2018), as can anaerobic ammonium oxidation (ANAMOX) (Hu et al., 2011). Flooded wetland areas often emit little N2O and can even be periodic N2O sinks, while drier non-ponded areas may represent more substantial sources (Tangen & Bansal, 2022).

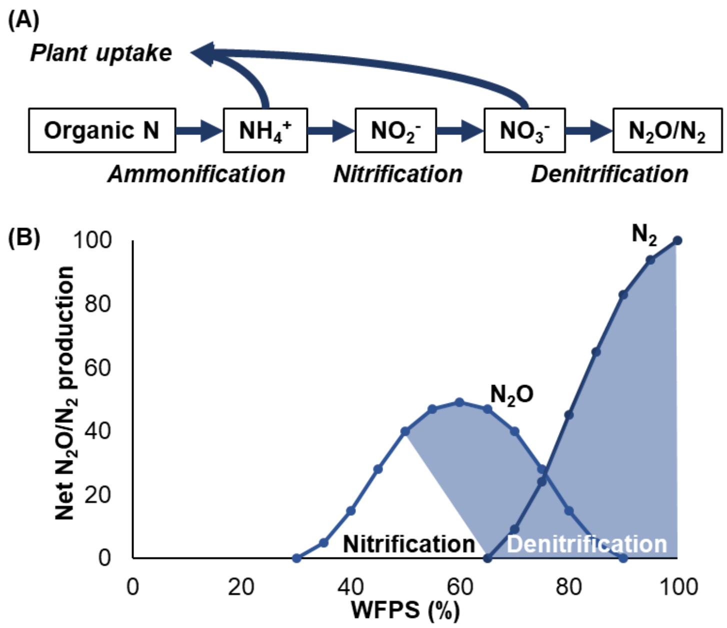

Figure 1: (A) Dominant nitrogen transformations in wetland soils, and (B) relationship between WFPS and N_2O/N_2 production, adapted from van Lent et al. 2015.Shaded blue areas indicate the dominance of denitrification versus nitrification.

Collectively, these, and other nitrogen transformation pathways can be influenced by plants and their inputs via several mechanisms. These include plant nitrogen uptake, leaf, root and shoot inputs that determine soil and sediment biogeochemistry and thus decomposition (Wieder et al., 2011; Girkin et al., 2019) with root exudates regulating rhizosphere properties and representing an important substrate for denitrification (Girkin et al., 2018). Root oxygen inputs control rhizosphere redox conditions (Girkin et al., 2020), and plant vascular tissues act as a potential soil to atmosphere egress pathway for N_2O produced in soils and sediments (Yu et al., 1997; Yamulki and Holt, 2017) (**Figure 1**). The interplay between these processes occurs within a spatially and temporally heterogeneous ecosystem and is further mediated by environmental variables including micro- and macro- topography, land use, and hydrology.

3. Plant regulation of tropical wetland N_2O emissions

Plants directly affect nitrogen availability in soils through root uptake of NH_4^+ and NO_3^-. In wetlands soils, nitrification can occur in surface soils under aerobic (non-flooded conditions) and close to roots that provide oxygen inputs (**Figure 2**) (Girkin et al., 2020). However, wetland plants have often been considered to mainly take up NH_4^+, as NO_3^- is often rapidly lost through denitrification. The precise balance of these processes varies between soil types, management and vegetation type (Kirk and Kronzucker, 2005). In general, tropical climates feature distinct dry and wet seasons which can result in flooding pulses in wetlands (Liengaard et al., 2013). This remains important for plants, as lowered water tables will aerate soils, driving nitrification, and thereby affecting the forms of nitrogen available for uptake (Barrios and Herrera, 1994). Plant litter inputs represent an important driver of soil N_2O emissions, but precise effects vary based on litter properties and the environment in which decomposition occurs (Wieder et al., 2011). Seasonally flooded soils in the Amazon have previously been shown to be rich in inorganic nitrogen, although much is subsequently lost during water table drawdown (Koschorreck, 2005). With the lowering of water tables, aquatic macrophytes can be left to decompose on draining wetland soils. In the Pantanal, Brazil, floating mats of *E. crassipes* have been proposed to release 300 – 1,000 kg N ha^{-1} yr^{-1}, approximately 10 times as much as carbon (Koschorreck, 2005; Sun et al., 2011). Phosphorus is often limiting in wetland soils (Cheesman et al. 2012), and low availability can limit the activity of nitrifying and denitrifying microbial communities (Yi et al. 2024). Combined, plant aboveground inputs therefore represent a major seasonal driver of N_2O emissions, equivalent to fertiliser applications in agroecosystems.

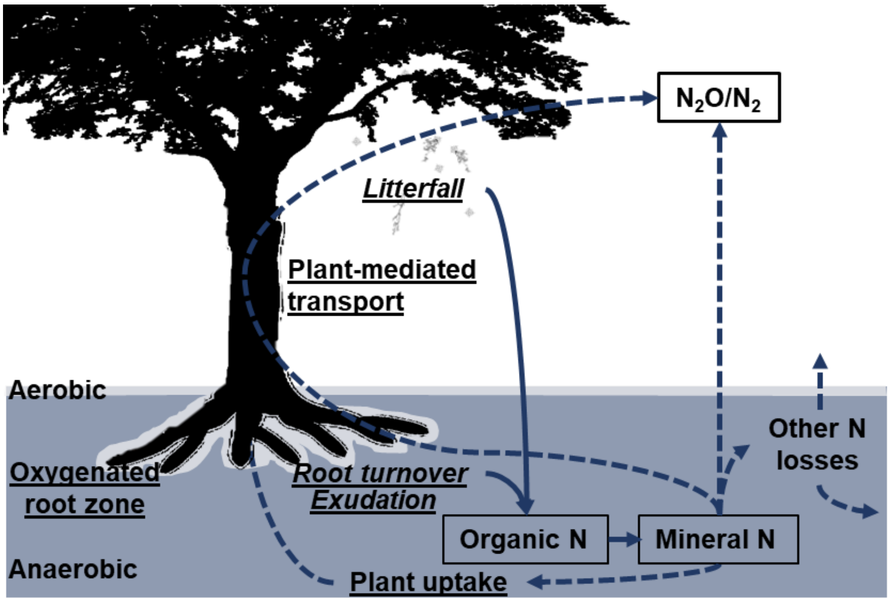

Figure 2: Plant-mediated controls over tropical wetland N_2O production, including plant-uptake of mineral nitrogen (N), plant litter inputs (leaf litterfall, root turnover), root exudation/rhizodeposition, plant-mediated transportation, and localised oxic zones around roots. Many key processes have been shown to be plant-species dependent.

Rhizodeposition can both directly, through providing carbon substrates required for denitrification, and indirectly, by determining rhizosphere properties, affect N_2O production. The largest component of rhizodeposition are root exudates, the composition of which depends on plant species, stage of development, soil properties, and prevailing environmental conditions (Badri and Vivanco, 2009). This is important as the extent of denitrification is known to depend on both the quality and quantity of the carbon input, with labile sugars driving generally greater rates of denitrification than more complex organic molecules (Dodla et al., 2008). Root exudate profiles for most tropical wetland tree species are entirely unknown, but in general evidence suggests that organic acids are present in 2:1 or 3:1 ratios with sugars for many tree species, with different ratios reported for other plant functional types (Girkin et al., 2018). Diurnal trends in N_2O fluxes have previously been reported in wetland ecosystems (Oktarita et al., 2017; Teh et al., 2017), and may be due to increases in plant inputs of carbon derived from photosynthesis during daylight hours, or due to changes in temperature between night and day, but this latter contrast is reduced in tropical ecosystems compared to temperate latitudes (Jauhiainen et al., 2014).

As well as being a substrate for the soil microbial community, litterfall, rhizodeposition and oxygen inputs can modify microbial community structure (Girkin et al. 2020), and thereby indirectly regulate the extent of N_2O production (Zhuang et al., 2020). The rhizosphere of wetland plant has previously been described as "oxic islands" which feature distinct microbial communities and diversity compared to bulk soils (Neori and Agami, 2016). However, few studies have investigated the abundance and function of tropical wetland plant rhizosphere microbial communities beyond rice. In general, nitrogen depletion in the rhizosphere, through uptake or loss of nitrate, and the exudation of low nitrogen compounds can work alongside optimising pH and redox potential to promote nitrogen fixation (Husson, 2012). The extent to which these processes differ between tropical wetland ecotypes, and different species, remains unclear.

Plant-mediated CH_4 transport has been widely reported in tropical wetland ecosystems, resulting in stem and canopy emissions, thereby contributing substantially to ecosystem scale dynamics (Pangala et al., 2017), but N_2O transport are less frequently assessed. Kreuzwieser et al., (2003) reported that the prop roots of *Rhizophora stylosa* emitted N_2O at a rate of 3.3 $\mu g\ m^{-2}$ root h^{-1}. Studies in temperate forested wetlands (Yamulki and Holt, 2017), and tropical dry forests (Welch et al. 2019) support the notion that some tree stems can be net N_2O emitters but highlight that soil emissions tend to dominate ecosystem fluxes. N_2O produced in the soil or dissolved in the porewater can be absorbed through the roots and transported through aerenchyma to aboveground tissues, where it is subsequently exchanged with the atmosphere. Evidence from studies of tropical wetland tree-emitted CH_4 suggest this process is mediated by a range of aboveground adaptations, including lenticels, and prop and knee-roots, with high and low emitting species further differentiated through contrasts in root inputs (driving GHG production), aerenchyma volume, and wood density (Sjögersten et al., 2019).

N_2O may also be produced during photosynthesis, from the reduction of NO_3^-, and during photo-assimilation of nitrite (NO_2^-) in chloroplasts (Smart and Bloom, 2001). Upper estimates suggest this may account for 5-6% of total N_2O emissions in agroecosystems, but there appears to be limited evidence of the importance of this process in wetland species (Yamulki and Holt, 2017).

4. Species-specific and ecotype controls

We have presented a range of sources of evidence that plants can exert multiple controls over the N_2O dynamics in tropical wetlands, but the extent to which processes differ between plant species and/or plant functional types, and the degree to which plant controls over fluxes are important relative to other processes, remains unclear. Few studies have assessed species-specific controls over N_2O emissions while controlling for other important regulatory processes (e.g. degree of flooding, management, and soil properties), and studies that have assessed such processes often have small sample sizes. Were and Hein (2021) reported no significant differences in N_2O emissions in the wet or dry season within a single Ugandan wetland site featuring *Typha latifolia, Phragmites mauritianus,* and *Cyperus papyrus*, with similar results reported elsewhere (Marín-Muñiz et al., 2015; Hernández and Junca-Gómez, 2020). However, such results may be because the studied species exhibit relatively similar adaptations to their environment, and therefore the relative differences in species-specific controls are small. Contrasting plant functional types (for example broadleaved evergreen trees, palms and mangroves in coastal wetlands) are possibly a more appropriate level at which to investigate differences in plant controls over emissions. Comer-Warner et al., (2022) reported significant differences in denitrification-derived N_2O from Melaleuca forest soils compared to mangrove soils in Vietnam, but greater potential rates of total denitrification (N_2O and N_2) in mangroves (8.1 ng N g^{-1} h^{-1}) than Melaleuca forest soils (6.8 ng N g^{-1} h^{-1}).

5. Impacts of global environmental change on N_2O dynamics

Tropical wetland ecosystems, and plant processes, are already significantly affected by climate and land use change. Across all tropical ecosystems, temperatures are likely to increase (IPCC, 2021), and more extreme weather events are predicted, including increased precipitation intensity (Endo et al., 2009), and more pronounced seasonality with lower precipitation during dry seasons but increases in wet seasons (Li et al., 2007). Collectively changes in precipitation will have significant consequences directly for N_2O production, primarily by affecting WFPS (van Lent et al., 2015). Climate change is also likely to have a significant impact on tropical wetland ecosystem productivity through CO_2 fertilisation effects impacting substrate availability, increased temperatures (also impacting the rate of microbial processes regulating N_2O pathways) (Raturi et al., 2022), and drought/extreme flooding (Malhi et al., 2014). The impacts of this combination of processes have rarely been investigated in tropical wetlands compared to other ecosystems, and at present limited tools and models are available which can account for the relevant processes and predict likely responses (Farmer et al. 2011). In general, N_2O emissions increase in line with primary productivity (Piñeiro-Guerra et al., 2019) of which temperature and moisture availability are major controls.

Land conversion has substantial consequences for GHG emissions from wetland ecosystems, by disturbing soils, changes in plant inputs, and alterations in management (van Lent et al., 2015). Drained peat soils can be a significant source of greenhouse gases (Girkin et al. 2023), including a substantial N_2O source due to lower pH, which inhibits N_2O reductase resulting in increased N_2O as the end project of denitrification rather than N_2 (Reddy & DeLaune, 2008). Measurements of N_2O fluxes from natural swamp forests can be up to 10 times lower than converted oil palm plantations due to plant fertiliser requirements and organic matter decomposition (Hergoualc'h and Verchot, 2014; Oktarita et al., 2017). Similarly, Iram et al., (2021) highlight substantial changes in N_2O emissions from land use change in coastal wetlands, with increased fluxes in drained pastures and adjacent sugarcane fields, particularly following fertilisation events (Iram et al., 2021). Castillo et al., (2017) demonstrated that N_2O emissions from deforested mangrove areas were up to 34 times greater than those from intact forest.

Conclusions

Tropical wetlands are a critical component of the global nitrogen cycle, representing a substantial organic nitrogen pool, but also a major source of N_2O emissions. Many of the underlying mechanisms driving emissions remain unclear, including how alterations in fundamental ecosystem processes (changes in vegetation type and inputs, including litter and rhizodeposition) and shifts in management will interact with climate change to affect emissions. Collectively, this hampers the ability to generate a new generation of models for determining and upscaling dynamics. Growing evidence suggests a high potential for feedbacks, from both land use and climate change, giving an urgent need for quantifying remaining underlying mechanisms of regulation, and identifying potential pathways for mitigation.

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