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Tree emissions of CH_4 and N_2O: Briefing and review of current knowledge

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Summary

This report reviews the available literature on methane (CH_4) and nitrous oxide (N_2O) release from plants (not soil) focussing on trees and the mechanisms for gaseous production, transport and exchange with the atmosphere to assess the significance of the role of trees in the global GHG budget. In summary, the existing evidence shows that emission of CH_4 and N_2O in trees can occur directly during aerobic production in tree stems and/or leaves and leaf litter, by microorganisms living inside the plant, or indirectly through transport in the stem of soil-produced gases. Gaseous transport of CH_4 and N_2O can occur through the aerenchyma[1] if present, or in dissolved form (particularly N_2O) through the movement of water in the xylem, and they can be emitted into the atmosphere from the stem surface, lenticels[2] , or via the stomata in leaf surfaces. Many factors have been reported to affect the production, transport and release of CH_4 and N_2O from trees, notably higher than ambient concentrations in the soil due to fertilisation or hydrological conditions, differences between tree species and UV radiation. However, robust tree emission data are scarce, particularly for mature trees, for conifer species, and for stems, shoots and leaves. Uncertainties are high but this flux component has been estimated as much as making a 10% contribution to the global CH_4 flux and 30% increase to the previously estimates of the N_2O budget. Most of the limited measurements available show the CH_4 and N_2O fluxes are low, compared to forest floor fluxes, but are not negligible and in some situations can be substantial, up to 14% and 18% for N_2O and CH_4 respectively, in Finnish Scots pine stands. Tree-mediated emissions from forested ecosystems are unaccounted for in current global CH_4 and N_2O budgets and are not included in the IPCC GHG Reporting Guidelines mainly due to the large uncertainties in the data on a global scale. This review highlights that although there is insufficient information particularly that relates to British forestry to generalise about the magnitude of the fluxes, there is enough evidence to show that these emission pathways do need to be quantified in order to draw up complete forest ecosystem budgets of N_2O and CH_4 fluxes. A better understanding of these fluxes, their drivers and magnitudes could be important if GHG accounting was modified in the future to include such potential sources.

Introduction

Over the past few years there have been several sudden increases in interest in the role that trees might play in the emissions of the key greenhouse gas of methane (CH_4) and to a lesser extent nitrous oxide (N_2O). These surges have been triggered by publication of novel results. The first such episode was the Keppler et al. (2006) paper on aerobic CH_4 emissions from leaves triggered by UV radiation and more recently the Bruhn et al. (2014) paper for N_2O. Other recent reports have been about emission of CH_4 and N_2O

[1] Aerenchyma are the air spaces that form in some plant tissues, particularly in stems and roots; often in response to anaerobic conditions, but their formation depends strongly on the plant species and conditions.

[2] Lenticels are macroscopic pores in stems and roots of woody plants that facilitate gas diffusion in and out.

from stems and leaves due to transport up from the soil (e.g. Rusch and Rennenberg, 1998; Pihlatie et al., 2005; Rice et al., 2010; Terazawa et al., 2007 and 2015; Covey et al., 2012; Machacova et al., 2013; Pangala et al., 2015 and Díaz-Pinés et al., 2016) and due to microorganisms living inside the tree (Covey et al., 2012). These reports have been followed by wider research and subsequently more clarity over processes and scale of emissions, but the topic continues to expand (e.g. Warner et al., 2017). It is timely therefore to produce a brief review of the key information on CH_4 and N_2O fluxes from trees.

It is well documented (Pangala et al., 2013) that many tree species, particularly those in anaerobic wetland ecosystems have the capacity to cope with soil anoxia through development of morphological adaptations such as hypertrophied lenticels, adventitious roots and enlarged aerenchyma which promote gas exchange between the atmosphere and the rhizosphere (Megonigal and Day, 1992; Kozlowski, 1997; Wang and Cao, 2012). In particular, if there is entry of O_2 to the root zone through pores then CH_4 can also enter the plant aerenchyma system and subsequently be emitted into the atmosphere (Laanbroek et al., 2010). Until recently the role of wetland plants as conduits for CH_4 emissions have mainly been investigated in numerous herbaceous species (for a review see Schütz et al., 1991; Singh and Singh, 1995; Bhullar et al., 2013) and for N_2O in a few species including rice (Reddy et al., 1989; Mosier et al., 1990) and rushes (Reddy et al., 1989). Rusch and Rennenberg (1998) stated that for most natural ecosystems the contribution of plant-mediated gas efflux to the total emission is unknown but depends on the soil and the plant community. For example, the contribution is of minor importance for ecosystems with low vegetation like Sphagnum dominated bogs where plants have no or only small roots (Thomas et al., 1996). In contrast, recent evidence shows that woody plants which have more gas occupying spaces in the stem xylem sapwood and heartwood (Gartner et al., 2004) and larger root systems can be a substantial source of both CH_4 and N_2O fluxes (e.g. Rusch and Rennenberg, 1998; Gauci et al., 2010; Rice et al., 2010; Machacova et al., 2013; Pangala et al., 2013; Díaz-Pinés et al., 2016) and arguably they are one of the least studied and well-understood emission pathways (Carmichael et al., 2014; Pangala et al., 2015). An example of the possible magnitude of CH_4 and N_2O fluxes is by Rice et al. (2010) who measured CH_4 emission from three woody riparian tree species of willow, ash and poplar grown in mesocosms and scaled it up globally using a leaf area normalized mean emission rate for flooded forest regions and estimated it to be 60±20 Tg yr^{-1}, which would be *ca.*10% of the global CH_4 source. Carmichael et al. (2014) synthesized the existing literature to provide a comprehensive estimate of the overall scale of vegetation in the global CH_4 budget including plant cisterns (water filled hollows and organs) that act as cryptic wetlands, heartwood rot in trees, the degradation of coarse woody debris and litter, or CH_4 transport through herbaceous and woody plants. They estimated, albeit with large uncertainty, that plant-based CH_4 emissions may represent up to 22 % of the total global CH_4 budget, contributing ca.32–143 Tg yr^{-1} with 6-42% (2-60 Tg CH_4 yr^{-1}) contribution from trees (Carmichael et al. 2014). Therefore, they emphasized the need to better resolve the role of vegetation in the biogeochemical cycling of CH_4 as an important contribution to closing the much-discussed gap in the global methane budget. Similarly for N_2O, tree stems and leaves may constitute a significant source of emission (Machacova et al., 2013; Pihlatie et al., 2005) and up to 30% higher than previously assumed emissions from plants have been

reported (Bruhn et al., 2014). The recent report of the Committee on Climate Change (2017) on estimating GHG emissions indicated that sectors with complex biological processes or diffuse sources such waste, agriculture and Land Use, Land Use Change and Forestry (LULUCF) have higher uncertainty level and therefore should be priority for further work. Nevertheless, global CH_4 and N_2O budget reports (e.g. Dlugokencky et al., 2011; Syakila and Kroeze, 2011; IPCC by Ciais et al., 2013) do not include plants as a distinct category of CH_4 and N_2O flux to the atmosphere due to concern regarding the uncertainties in emissions on a global scale.

Unfortunately, comparison of the gas fluxes reported by different studies is complicated because of the wide variety of plant material, experimental conditions and measurements techniques. In addition, several different flux units are used, and results can sometimes be expressed on a ground, stem or leaf area basis, and due to the measurement techniques are rarely measured at the stand or forest scale. In this review I have left the units as they were reported but tried where possible to convert units to the same basis in Appendix 2, and to clarify what area basis was used.

Mechanisms responsible for N_2O and CH_4 formation and emissions

Several authors have attempted to identify the mechanisms responsible for plant-mediated GHG emissions but until recently most of these investigations were made on seedlings and plants other than trees. The methods by which CH_4 and N_2O may be emitted or produced from above-ground plant surfaces in general were summarised by Machacova et al. (2013) to be: i) by soil microorganisms and the subsequent diffusion into and transport within the plant (Chang et al., 1998; Rusch and Rennenberg, 1998; McBain et al., 2004; Dueck et al., 2007; Wang et al., 2008; Nisbet et al., 2009), ii) by microorganisms living inside the plant (Zeikus and Ward, 1974; Bosse and Frenzel, 1997; Raghoebarsing et al., 2005; Prendergast-Miller et al., 2011), and iii) by the plant itself (Zhang et al., 2000; Smart and Bloom, 2001; Keppler et al., 2006 and 2008; McLeod et al., 2008; Vigano et al., 2008; Wang et al., 2008 and 2013; Brüggemann et al., 2009; Nisbet et al., 2009; Bruhn et al., 2014). These pathways are shown in Figure 1, overleaf.

Indirect emission of gases taken up from soil/water via different uptake and loss routes

CH_4 and N_2O produced in the soil or dissolved in groundwater can be absorbed by roots and transported in stems through aerenchyma or the xylem to the above-ground organs by the transpiration stream and exchange with atmosphere via the stem surface, lenticels and/or leaf stomata (e.g. Rusch and Rennenberg, 1998; Chang et al., 1998; Pihlatie et al., 2005; Terazawa et al., 2007; Machacova et al., 2013; Carmichael et al., 2014; Díaz-Pinés et al., 2016). For woody plants in particular, lenticels seem to be the

most important site of gas exchange between the plant's intercellular aerenchyma system and the atmosphere (Buchel and Grosse, 1990; Machacova et al., 2013).

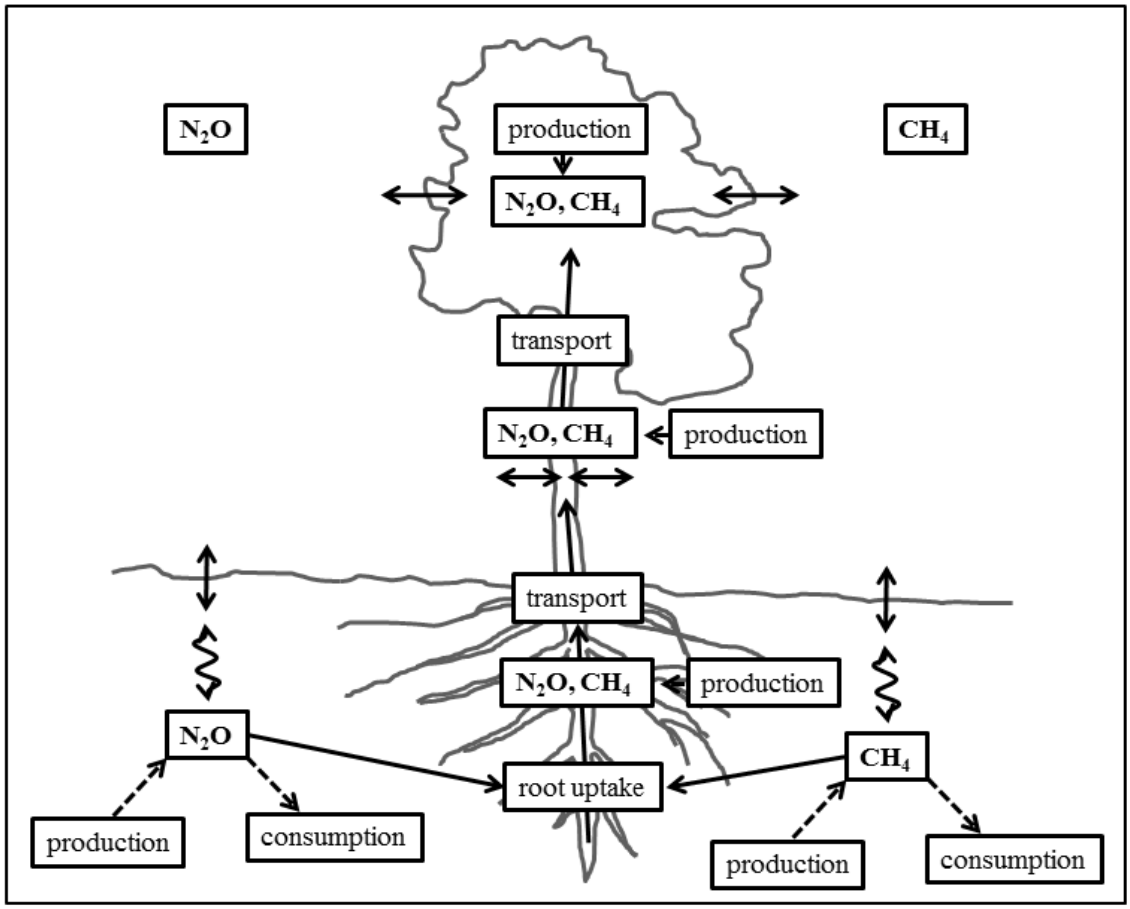

Figure 1: From Machacova et al. 2016, schematic illustration of N_2O and CH_4 fluxes in soil-tree-atmosphere continuum.

Terazawa et al. (2007) measured CH_4 emissions from the stem surfaces of mature ash trees in a floodplain forest in northern Japan and explained the source of CH_4 emitted to be the dissolved CH_4 in groundwater especially because concentrations up 10,000 times higher than atmospheric CH_4 were observed. They concluded that CH_4 transport from the submerged soil layer to the atmosphere may occur through internal air spaces in tree bodies.

Whilst there have been some studies on the emission of CH_4 and N_2O from wetland forest species which are naturally adapted to flooding by the formation of aerenchyma and lenticels, the emissions from GHGs dissolved in transpiration water of tree species lacking an aerenchyma system (particularly mature trees) is still an overlooked pathway.

Direct emission of gases formed in stem by microorganisms living inside (or outside) the plant or through microbial decay

A second potential mechanism of CH_4 fluxes from stems may be lateral diffusion of microbially derived CH_4 produced within the stem itself (Werner et al., 2017). Microorganisms such as archaeal methanogens can colonize inside the wood of living trees and produce CH_4 (Zeikus and Ward, 1974; Zeikus and Henning, 1975; Van Der Kamp et al., 1979; Xu and Leininger, 2001; Schink and Ward, 1984; Mukhin and Voronin, 2011; Covey et al., 2012; Wang et al., 2016) even without obvious signs of infection on the bark surface i.e. rot or not (Wang et al., 2016; Werner et al., 2017). This biotic mechanism has largely been ignored, yet conditions that promote anaerobic activity in living wood, and hence potentially CH_4 production, are prevalent across forests (Covey et al., 2012). According to Covey et al. (2012) in low O_2 and high CO_2 environments, such as those in tree trunks (Teskey et al., 2008), the aerobic syntrophic (i.e. "feeding together") consortia of heart-rot fungi, bacteria and archaea are capable of breaking down complex biopolymers that individual organisms cannot digest (Bryant et al., 1967) leading to degradation of wood and production of CH_4 e.g. in timbers stored under conditions similar to those found inside living trees (Krüger et al., 2008; Beckmann et al., 2011). They also indicated that even in predominately aerobic environments, fungal metabolism can lead to anaerobic microsites and the formation of large quantities of CH_4 by archaea (Reith et al., 2002). Furthermore their data for a NE American deciduous forest revealed that trunk-gas CH_4 concentrations can be many times that of atmospheric for both lowland and upland tree sites. The highest concentrations were found for the upland site, and in species known to be susceptible to heart rot, suggesting this disease as the mechanism for CH_4 production. They concluded that although the common infection of trees by heart rot fungus, and associated bacteria and archaea, has long been a concern of commercial forestry it also plays an important role in understanding the role of forests in the global CH_4 budget. For N_2O, Prendergast-Miller et al. (2011) demonstrated N_2O production by filamentous fungi and ectomycorrhizal fungi in pure culture and indirectly in forest soils from nitrate reduction.

Direct emission of gases produced in the plant

Although it has been debated by Schiermeier (2009), CH_4 and N_2O gases have been reported to be produced by plants through aerobic production in live trees and/or leaves and leaf litter (Keppler et al., 2006; McLeod et al., 2008; Keppler et al., 2009; Keppler 2010; Bruhn et al., 2012). Nisbet (2009) argued that plants do produce small amounts of CH_4 if grown in unnaturally high temperatures or strong ultraviolet light but he believed that rather than being a result of plant metabolism, this gas is a by-product of the breakdown of cell material (Schiermeier, 2009). Nevertheless, a number of processes have been reported to be responsible for GHG formation within plants that can ultimately be released into the atmosphere. Keppler et al. (2008) identified an aerobic mechanism of CH_4 production from degradation of the methoxyl groups of pectin in plant cell walls and showed a strong dependence on temperature and exposure to light, in particular in the UV waveband indicating that plant material can be an important direct source of CH_4 emissions. Employing ^{13}C-labeled methionine, Lenhart et al. (2015) clearly

identified the sulfur-bound methyl group of the amino acid L-methionine as a carbon precursor of CH_4 released from lavender. Furthermore, when lavender plants were stressed physically, CH_4 release rates and the stable carbon isotope values of the emitted CH_4 greatly increased. They concluded that plants possess a mechanism for CH_4 production and suggested that methionine might play an important role in the formation of CH_4 in living plants, particularly under stress conditions. While this observation has not been repeated in other plant groups, it might be assumed to be a common feature.

N_2O has been reported to be produced enzymatically during photosynthesis from NO_3 reduction and during photoassimilation of nitrite (NO_2^-) in the chloroplast inside leaves of wheat (Dean and Harper, 1986; Smart and Bloom, 2001; Hakata et al., 2003). 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. There appears to be no literature for this mechanism from trees but seems likely to happen as it is a fundamental part of N assimilation and photosynthetic metabolism.

McLeod et al. (2008) studied the role of ultraviolet (UV) radiation in the formation of CH_4 (and other trace gases) from plant pectins *in vitro* under aerobic conditions and from leaves of tobacco. Their results demonstrated production of CH_4 (also ethane and ethylene) from the methyl ester groups of pectin and that reactive oxygen species (ROS) arising from environmental stresses have a potential role in mechanisms of CH_4 formation although rates of CH_4 production were lower than those previously reported for intact plants in sunlight. Similarly, according to Bloom et al. (2010) the global foliar CH_4 emissions from UV-irradiated pectin could account for <0.2% of global foliar CH_4 emissions with 0.2-1.0 Tg yr^{-1}, of which 60% would be from tropical latitudes.

More recently the role of UV on N_2O emissions has also been investigated by Bruhn et al. (2014) from grass covered soils and in the laboratory from fresh grass and tree leaf materials (plane, maple and hazel) exposed to solar irradiance with and without UV-screening. They found that N_2O was emitted at rates on average 12-times higher in response to artificial UV-B and 7-times higher in response to natural sunlight, mostly caused by the UV waveband rather than the photosynthetically-active part of the spectrum, and that the prevailing zone for the N_2O formation appeared to be at the very surface of leaves. Emission response to UV-A was of the same magnitude as that to UV-B and therefore they indicated that UV-A is more important than UV-B given the natural UV-spectrum at Earth's surface. Based on their measurements they concluded that real emission rates of N_2O may be up to *ca.*30% higher than previously estimated in natural UV radiation conditions, as UV is excluded in the typical dark chamber flux measurements and emissions from plants are usually not included in N_2O budgets.

Flux magnitudes and effects of environmental factors

The previous sections have shown that plant surfaces (stem and/or leaf) can both emit and take up CH_4 and N_2O and these fluxes can significantly contribute to the net ecosystem exchange of these gases (e.g. Pangala et al. 2013, Machacova et al., 2013; Maier et al., 2016). However, the flux magnitudes depend on many factors. Measurements show that soil structure, soil water content, redox potential in the rooting

space , soil temperature, soil pore water CH_4 concentration, soil fertilisation and root N_2O and CH_4 concentrations, vegetation type, stem diameter and wood specific density, plant age, PAR and UV radiation and primary productivity all influence the observed rates (see cited references in Appendix 1). It is difficult to explore each of these factors separately because of the large interactions between them, different effects on plant components i.e. on stem and leaves, large variations and uncertainties in the measurements and emission rates. Therefore, this review explores the main factors relevant to forestry and gives examples of the literature variations that may be important for measurement techniques, quantification at the ecosystem level and for future assessment of global budgets. Results from key papers measuring CH_4 and N_2O fluxes from trees are summarised in Appendix 2. In order to understand the size of the flux measurements quoted, some very approximate scaling can be done. For measurements on a tree stem area basis, and making the following simplistic assumptions: tree diameter = 20 cm; height = 20 m; cylindrical stem (ignoring branches); flux independent of height and time; and stem density = 500 ha^{-1}; then 1 μmol m^{-2} h^{-1} = 0.9 kg CH_4 ha^{-1} y^{-1}, and in CO_2 equivalents = 22 kg CO_2e ha^{-1} y^{-1}. If the rate is 1 μmol m^{-2} h^{-1} expressed per unit leaf area then assuming a value of leaf area index (LAI[3]) = 5, the equivalent per hectare is 7 kg CH_4 ha^{-1} y^{-1} and in CO_2 equivalents = 175 kg CO_2e ha^{-1} yr^{-1}. Note that for comparison, CH_4 emissions from soils are typically in the range -20 (i.e. uptake), 40 and 100 kg CO_2e ha^{-1} yr^{-1} for standing forest on mineral, organo-mineral and peat soils respectively (Morison et al. 2012, median values from Table 4.5, p.51).

Stem height

Emissions of CH_4 and N_2O can vary with stem height and usually seem to reduce with height above the ground, implying that there is a below-ground root or soil source. The study of Terazawa et al. (2007) mentioned earlier on CH_4 emissions from the stem surfaces of mature Japanese ash trees in a floodplain forest showed positive CH_4 fluxes throughout their study period, including the leafless season with much higher mean flux (176 μg CH_4 m^{-2} stem surface h^{-1}) at the lower stem position (15 cm above the ground) than the upper (70 cm above the ground) stem positions (97 μg CH_4 m^{-2} stem surface h^{1}, Appendix 2). Similarly for N_2O, Díaz-Pinés et al. (2016) measured emissions from stems of upland European ash and both mature and young European beech after soil fertilization using static chambers fixed at different heights on the stem. Their results showed stem emissions decreased linearly with increasing height with a mean flux of 15.1 and 8 μg N_2O-N m^{-2} bark h^{-1} at height 20 cm and 130 cm respectively above soil level (maximum 80 μg N_2O-N m^{-2} bark h^{-1} at 20 cm) from the beech tree but at 200 cm, stem N_2O emissions were below the detection limit. Similarly for the ash tree, mean stem emissions at both heights were 14.5 and 4.5 μg N_2O-N m^{-2} bark h^{-1} respectively.

Seasonal, temporal and spatial variations

At present data are very scarce on the effect of seasonal, diurnal and spatial variations and controls on the magnitude of tree-mediated GHG emissions especially for mature forests (Terazawa et al., 2015; Pangala et al., 2015; Machacova et al., 2016) and on the

[3] area of leaves per unit area of ground, typical range for forests 2-8

emission rates of tree species that do not have an aerenchyma system (Pihlatie et al., 2005; Machacova et al., 2013; Díaz-Pinés et al., 2016).

Recently Terazawa et al. (2015) performed field measurements in a temperate wetland forest in northern Japan to assess the spatial and temporal variability in CH_4 emissions from stem surfaces of mature ash trees. They showed daytime stem emission rates varied between 81 and 1,305 μg CH_4 m^{-2} stem surface h^{-1} among individual trees and showed a spatial gradient apparently corresponding to the difference in water table depth at the experimental site (Appendix 2). Furthermore, they showed high variability in stem CH_4 emissions in space and time and the importance of soil temperature, water table depth and soil pore water CH_4 concentration as possible environmental factors controlling stem CH_4 emissions. Contrary to this Warner et al., (2017) measured CH_4 fluxes from soils, coarse woody debris, and tree stems over the growing season in an upland temperate forest in the east of US and found no influence of precipitation or soil moisture on the spatial and temporal variability of stem CH_4 fluxes. Their results showed that tree stems were a net CH_4 source (up to 0.98 nmol m^{-2} s^{-1}), with a mean of 0.11 ± 0.21 nmol m^{-2} s^{-1} (across all species) and significant differences depending on tree species. Stems of black gum, beech, and tulip tree consistently emitted CH_4, whereas stems of red maple, black birch, and oak species were intermittent sources. Their results demonstrated the importance of CH_4 emissions from living stems in upland forests and the need to consider multiple forest components to understand and interpret ecosystem CH_4 dynamics. Gauci et al. (2010) measured average CH_4 emissions from mature wetland alder tree stems in England ranging from 4 μg m^{-2} stem surface h^{-1} in May to 101 μg CH_4 m^{-2} stem surface h^{-1} in early October, amounting to approximately 20% of the measured CH_4 flux from the soil surface.

The effect of spatial and temporal variability in stem CH_4 emissions and their controls have also been examined by Pangala et al. (2015) in situ in two wetland-adapted tree species (alder and birch) in an English wetland. They demonstrated that tree-mediated CH_4 emissions contributed up to 27% of seasonal ecosystem CH_4 flux with the largest relative contributions occurring in spring and winter. Emissions varied significantly between the two tree species, with alder displaying minimal seasonal variations, while substantial seasonal variations were observed in birch. Furthermore, they reported that trees from each species emitted similar quantities of CH_4 from their stems regardless of whether they were situated in wetland surface hollows or hummocks. Their results also showed that soil temperature and pore-water CH_4 concentrations best explained the seasonal variability in stem emissions, while wood-specific density and pore-water CH_4 concentrations best accounted for between-species variations in emission.

Covey et al., (2012) found average, growing season, trunk-gas CH_4 concentrations >15,000 ppm in common well-drained upland, temperate-forest species (red maple, red oak, black birch). Trunk CH_4 concentrations were 2.3-times higher in trees of upland habitat, where heart rot is expected to be more prevalent than at lowland sites (Basham, 1973). More importantly, they indicated that upland soils typically consume rather than produce CH_4 (Bradford et al., 2001), suggesting that the bulk of the trunk CH_4 was produced internally and did not accumulate via soil-tree diffusion pathways. Scaling up their results they estimated emission rate of 52 ± 9.5 ng CH_4 m^{-2} s^{-1}; indicating that these rates were of a similar magnitude to the soil CH_4 sink in temperate forest, and equivalent in global warming potential to ~18% of the carbon likely sequestered by their

forest. CH_4 in situ emissions from trunks of upland poplar forest in Beijing (Wang et al., 2016) showed large temporal and spatial variability. Emissions were much higher in the growing season than when dormant and were linearly correlated with air and soil temperatures. In their study CH_4 emissions at the height of 130 cm were in the range of c. 0-200 μg m^{-2} h^{-1} on a trunk surface area basis, with annual mean emissions of 85.3 and 103.1μg m^{-2} h^{-1} in their upper and lower measurement plots, respectively. They also observed large spatial variations within each plot area with CVs of the CH_4 emissions ranging from 19% to 68% in the upper plot and from 22% to 54% in the lower plot. More recently, Pitz and Megonigal (2017) measured CH_4 emissions from stems of mature, temperate, deciduous, upland forest in the US from a number of species (tulip tree, beech, mockernut hickory, oak, chestnut oak, red maple and American sweetgum) using both the traditional static-chamber method and a new high-frequency, automated in situ system. They reported fluxes ranging from < -0.07 μmol CH_4 m^{-2} tree stem h^{-1} to an order of magnitude higher in June (9.53 ± 2.87 μmol CH_4 m^{-2} tree stem h^{-1}), during an event of uncertain duration. Tree emissions averaged across 68 observations on 17 trees from May to September were 1.59 ± 0.88 μmol CH_4 m^{-2} stem h-1, while soils adjacent to the trees consumed atmospheric CH_4 at a rate of -4.52 ± 0.64 μmol CH_4 m^{-2} soil h^{-1}. Interestingly, their high-frequency measurements revealed diurnal patterns in the rate of tree-stem CH_4 emissions which points to soils as a source of CH_4 and transpiration as a possible driver of CH_4 fluxes. However, the absence of correlations with soil water content or water table depth in their study is consistent with a microbial source inside these trees. Pits and Megonigal (2017) calculated with a conservative scaling exercise that tree stem CH_4 emissions offset 1-6% of the annual CH_4 consumption by soils, and under certain circumstances the emissions may be large enough to briefly convert a forest from a net CH_4 sink to a net source. Their results certainly add to the growing body of evidence to suggest that forests are not uniform consumers of CH_4. It emphasises that in order to make progress in this area of research it will be necessary to use high frequency measurement techniques, given the spatial and temporal variations of these fluxes.

Rooting zone gas concentration and hydrology

Net stem fluxes can be dictated by higher-than-ambient concentrations of CH_4 and N_2O in the root zone as a result of e.g. fertilisation (mainly for N_2O) and hydrology (mainly for CH_4) which promote soil microbial processes, increasing and decreasing fluxes with rising and falling water table height (e.g. Pangala, 2013; Terazawa et al., 2015; Warner et al., 2017).

Rusch and Rennenberg (1998) were some of the first to measure CH_4 and N_2O fluxes between tree stems and atmosphere, using controlled conditions in three-year-old seedlings of black alder. They observed both CH_4 and N_2O were emitted through the bark of the stem into the atmosphere when the root zone concentrations of the gases were higher than ambient concentrations. Immediately after flooding of the soil, N_2O was emitted from the seedlings' bark at a rate of 350 μmol N_2O m^{-2} h^{-1} whereas CH_4 flux could not be detected. After more than 40 days of flooding CH_4 fluxes up to 3750 μmol CH_4 m^{-2} h^{-1} from the stem were measured, while N_2O emission had decreased below the limit of detection. They concluded that flooding of the soil caused a decrease in N_2O emission but an increase in CH_4 efflux from the stem. In their study CH_4 and N_2O

effluxes also decreased with increasing stem height and correlated with gas mixing ratios in the soil, indicating diffusion through the aerenchyma from the roots as the major path of gas transport. Therefore they concluded, for the first time, that woody species with aerenchyma can serve as conduits for soil-derived trace gases into the atmosphere.

Machacova et al. (2013) compared the emissions of CH_4 and N_2O from stems of riparian black alder, and non-riparian beech trees, as affected by flooding. Flooding caused a dramatic transient increase of N_2O stem emissions by factors of 740 for alder and up to 14,230 for beech, demonstrating for the first time that beech trees such can emit significant amounts of N_2O from their stems despite lacking aerenchyma. However, in their study stem emissions of CH_4 were low compared with N_2O and uptake was even measured in the beech control treatments. Their results suggested that CH_4 was transported mainly through the aerenchyma, whereas N_2O transport occurred in the xylem sap. More recently Machacova et al. (2016) also showed for the first time that mature Scots pine trees in a boreal forest stand in southern Finland consistently emitted N_2O and CH_4 from both stems and shoots with higher stem N_2O and CH_4 fluxes from trees in wet than from those in dry areas of the forest. For CH_4, the median stem fluxes at the wet plot (0.100 µg CH_4 m^{-2} stem h^{-1}) were one order of magnitude higher than those at the dry plot (0.013 µg CH_4 m^{-2} h^{-1}, Appendix 2). Moreover, the shoot fluxes of N_2O and CH_4 exceeded the stem flux rates by 16 and 41 times, respectively. In their dry field conditions N_2O stems and shoots emitted at rates (median values) of 0.023 and 0.097 µg N_2O per m^{-2} (of stem & projected leaf area) per h^{-1} respectively. The corresponding CH_4 emission rates were 0.005 and 0.050 µg CH_4 m^{-2} h^{-1}, respectively. Scaling up these emission rates to per hectare at stand level they estimated stem and shoots fluxes up to 0.11 mg N_2O ha^{-1} h^{-1} and 1.9 mg N_2O ha^{-1} h^{-1}, respectively, for N_2O and 0.03 and 1.1 mg CH_4 ha^{-1} h^{-1} for CH_4. For their wet plot scaling up emissions from stem and shoots were 0.20 and 3.3 mg N_2O ha^{-1} h^{-1}, respectively, for N_2O and 0.59 and 24 mg CH_4 ha^{-1} h^{-1}, for CH_4. Fluxes of N_2O at the dry and wet plots were equivalent to 8% and 18% of the forest floor emission respectively. Interestingly, whereas trees were a source of CH_4, the forest floor was a sink in the dry plot. The contribution of CH_4 in their wet plot to the forest floor was 14%. Therefore they concluded that N_2O release from boreal pine forests may be underestimated and the uptake of CH_4 may be overestimated when ecosystem flux calculations are based solely on forest floor measurements.

Maier et al. (2016) measured gas fluxes of N_2O and CH_4 at stem and soil levels simultaneously from a well aerated and a loamy-clay soil of two European mountain beech forests. Measurements were made using static chamber systems and gas chromatography and continuous laser analyses. Contrary to the study of Machacova et al. (2013) their results showed beech stems mostly took up N_2O from the atmosphere at both sites, whereas CH_4 was emitted. They concluded that tree stem and soil fluxes were affected by soil structure, soil water content and the redox potential in the rooting space and that trees might provide preferential pathways for GHGs produced in the subsoil. CH_4 can also be emitted from leaves as a result of high water table as demonstrated by Rice et al. (2010) who reported from a greenhouse mesocosm study significant emissions of anaerobically soil produced CH_4 transmitted to the atmosphere (0.6 to 2.3 mg CH_4 m^{-2} ground area h^{-1}, Appendix 2) through three broadleaf riparian tree species grown under flooded conditions.

With regards to gas concentration in the rooting zone, Pihlatie et al. (2005) measured plant-mediated N_2O emissions from the leaves of potted European beech seedlings after fertilizing the soil with ^{15}N-labelled ammonium nitrate ($^{15}NH_4$ $^{15}NO_3$), and after exposing the roots to elevated concentrations of N_2O. They found that fertiliser induced N_2O+$^{15}N_2O$ emissions from beech leaves. Likewise, the foliage emitted N_2O after beech roots were exposed to elevated concentrations of N_2O. The average N_2O emissions from the fertilization and the root exposure experiments were 0.4 and 2.0 µg N_2O-N m^{-2} leaf area h^{-1}, respectively. As with emissions from tree stems, higher than atmospheric concentrations of N_2O in the leaves of the forest trees may indicate potential for canopy N_2O emissions in the forest. Similarly for CH_4, the study of Díaz-Pinés et al. (2016) mentioned earlier on upland European ash and beech conducted simultaneous field measurements of stem and soil N_2O emissions after different fertiliser applications to test whether stem N_2O emissions were occurring under those varying conditions. Before soil fertilization, the baseline stem N_2O emissions were at most 2 µg N_2O-N m^{-2} bark h^{-1} (Appendix 2). After fertilization, stem and soil emissions were linearly correlated and both the beech and the ash stems N_2O emissions reached a maximum of 80 and 35 µg N_2O-N m^{-2} bark h^{-1} respectively. The effect of tree species and age on the amount of N_2O released by tree stems and its contribution relative to soil N_2O emissions was also investigated. They observed as in the study of Machacova et al., (2013) that N_2O emissions from stem can occur even without aerenchyma, as a result of xylem water transport. However, in their study the stem N_2O emissions represented only 1-3 % of total N_2O emissions from both the soil and stem at the forest level. They indicated that if this holds for other forest ecosystems, stem N_2O emissions would be a minor pathway of N_2O loss from terrestrial ecosystems into the atmosphere.

UV radiation

Leaf emissions N_2O have also been measured in response to natural sunlight due to UV radiation for from grass and trees by Bruhn et al. (2014) with rates of c. 20-50 nmol m^{-2} h^{-1}, mostly were due to the UV-A and UV-B components. Sundqvist et al. (2012) conducted semi-continuous field measurements on branches of Norway spruce, birch, rowan and pine at a forest site in central Sweden to study direct CH_4 exchange by plants and its dependence on photosynthetically active radiation (PAR), ultraviolet radiation (UV-radiation), temperature and photosynthesis. In contrast to the previous studies their results showed a net uptake of CH_4 by all the studied plants. The average CH_4 uptake per unit of leaf area across all species and environmental conditions was 0.7 µmol m^{-2} h^{-1}. When this value was scaled up using the leaf area index for their forest, they estimated a value of 3.4 µmol m^{-2} h^{-1} which is close to the mean CH_4 soil oxidation rate of 4.0 µmol m^{-2} h^{-1} in various forest soils based on 28 studies (Jang et al., 2006). This indicates that the canopy might play an equally important role as the soil in the global context. Moreover, they observed significant correlation between CH_4 flux and PAR or and UV-radiation with increasing CH_4 uptake at higher values of PAR at UV-radiation.

Conclusions

It is clear that plant-mediated CH_4 production, transport and emission through different parts of plants into the atmosphere is a significant source, but robust tree emission data are scarce, particularly for mature trees growing in non-waterlogged conditions, tree species lacking aerenchyma, conifer species, and for stems, shoots and leaves. Uncertainties in emission estimates are high particularly for N_2O as it is less well studied but fluxes are not negligible, and emissions have been reported to occur from trees whilst the soil is a net sink. Thus, for neither gas do we know enough to be able to estimate the contribution of either stem or leaf emissions/uptake for forest GHG budgets. Therefore, more measurements required, in situ, and in particular for conditions typical of the extensive areas of British forestry to i) characterise and quantify CH_4 and N_2O fluxes, ii) investigate the source and transport mechanisms of fluxes from trees in the continuum soil-tree-atmosphere, iii) determine the relationships between CH_4 and N_2O fluxes and environmental parameters such as temperature, moisture, radiation and environmental stress. Experimental techniques utilizing transparent flux chambers measurements (particularly for N_2O emission in response to UV radiation) of leaf, stem (including shoots or branches) and soil floor (including vegetation), and/or stable isotopes will be important to identify source strength and variability of fluxes and for future estimation of the role of forests in the CH_4 and N_2O budgets for inventories.

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Appendix 1:

Main factors affecting CH_4 and N_2O emissions from plants reported in the literature

Soil water content	Rusch and Rennenberg, 1998; Yan et al., 2000; Machacova et al., 2013; Terazawa et al., 2015
Soil structure, Redox potential	Maier et al., 2016
Soil temperature	Sundqvist et al., 2012; Terazawa et al., 2015
Soil pore water CH_4 concentration	Pangala et al., 2p013; Terazawa et al., 2015
Soil fertilisation and CH_4 and N_2O concentrations in the rooting zone	Rusch and Rennenberg, 1998; Pihlatie et al., 2005; Díaz-Pinés et al.; 2016
Vegetation type	Chen et al., 2002; Zou et al., 2005; Rusch and Rennenberg, 1998; Díaz-Pinés et al., 2016
Stem diameter	Pangala et al., 2013; Machacova et al., 2016
Wood specific density	Pangala et al., 2013
Plant age	Butterbach-Bahl et al., 1997
PAR and UV radiation	McLeod et al., 2008; Sundqvist et al., 2012; Bruhn et al., 2014
Primary productivity	Sundqvist et al., 2012

Appendix 2:

Summary of the reported CH_4 and N_2O emissions from tree stems and leaves under a variety of conditions

Tree species	experimental situation	Author	Measured Fluxes	Experimental condition
red maple *(*Acer *rubrum),* red oak *(Quercus rubra),* black birch *(Betula lenta)*	Upland well-drained, temperate-forest species (in situ)	Covey et al (2012)	11.7 (umol CH_4 m^{-2} h^{-1}) (m^{-2} ground area, scaled using wood volume)	Pre leaf out (April) and post leaf out (July)
alder *(Alnus glutinosa)*	temperate forested wetland, Riparian	Gauci et al. (2010)	0.25 to 6.3125 (umol CH_4 m^{-2} stem area h^{-1})	May to early October respectively
alder (*Alnus* glutinosa) and betula (Betula pubescens)	temperate forested wetland, Riparian Mature trees Young trees	Pangala et al. (2015)	 4.2 (umol CH_4 m^{-2} stem area h^{-1}) 8.7 2.2 2.2	Total of spring, summer, autumn and winter measurements 3m tree height 10m tree height 3m tree height 10m tree height
poplar *(Populus davidiana)*	Upland forest	Wang et al. (2016)	0–12.5 (umol m^{-2} stem area h^{-1})	

			annual mean emissions of 5.331 and 6.444 on upper and lower plots, respectively	
black alder *(Alnus glutinosa)*	3 yr old seedling in pots containing soil from an alder swamp	Rusch & Rennenberg (1998)	CH_4 was negligible 350.0 (umol N_2O m^{-2} stem area h^{-1}) 3750 (umol N_2O m^{-2} stem area h^{-1}) negligible N_2O	directly following flooding, 40 days after flooding
ash *(Fraxinus mandshurica)*	Mature trees in floodplain forest	Terazawa et al. (2007)	11.0 (umol CH_4 m^{-2} stem area h^{-1}) 6.1 Equivalent to 6.875 (umol CH_4 tree h^{-1}) (eq. to 0.169 umol CH_4 m^{-2} forest ground area h^{-1})	stem height above the ground 15cm 70cm total mean height of 5-80cm above ground
ash *(Fraxinus mandshurica)*	Mature trees in floodplain forest	Terazawa et al. (2015)	5.06 to 81.56 (umol CH_4 m^{-2} stem area h^{-1}) 5.06 to 32.0 >50	Day time spatial variation range at 15cm stem height trees at water table depth 100cm below soil surface trees at water a few cm near the surface

beech *(Fagus sylvatica)* ash *(Fraxinus angustifolia)*	Upland	Díaz-Pinés et al. (2016)	Maximum 0.07 (umol N_2O m^{-2} stem area h^{-1}) Mean 0.54 (maximum 2.857) Mean 0.29 Mean 0.52 (maximum 1.25) Mean 0.16 below detection limit	Before fertilisation After fertilisation 20cm above soil 130cm above soil 20cm above soil 130cm above soil 200 cm above soil
black alder *(Alnus glutinosa)* beech *(Fagus sylvatica)*	Riparian mesocosms in greenhouse Upland	Machacova et al. (2013)	0.18 (umol N_2O m^{-2} stem area h^{-1}) 0.06 (umol CH_4 m^{-2} stem area h^{-1}) 132.86 (umol N_2O m^{-2} stem area h^{-1}) 1.27 (umol N_2O m^{-2} stem area h^{-1}) 3.53 (umol CH_4 m^{-2} stem area h^{-1}) 0.007 (umol N_2O m^{-2} stem area h^{-1}) 0.125 (umol CH_4 m^{-2} stem area h^{-1}) and even deposition 56.84 (umol N_2O m^{-2} stem area h^{-1}) 103.52 umol N_2O m^{-2} stem area h^{-1}) 0.12 umol CH_4 m^{-2} stem area h^{-1})	before flooding short term after flooding after 8 days from flooding before flooding after 1 day of flooding after 2nd day of flooding 3rd day after flooding

Scots pine (*Pinus sylvestris)*	boreal forest	Machacova et al. (2016)	median 0.00052 (umol N_2O per m^{-2} stem area h^{-1}) Median 0.0022 (umol N_2O per m^{-2} shoot projected leaf area h^{-1}) Median 0.000313 to 0.000813 (umol CH_4 m^{-2} stem area h^{-1}) Median 0.00313 (umol CH_4 m^{-2} shoot h^{-1}) Median 0.00625 umol CH_4 m^{-2} stem area h^{-1})	Dry plots Stem shoot Stem Shoot Stem - Wet plots
beech *(Fagus sylvatica)*	Leaves of potted trees	Pihlatie et al. (2005)	0.014 to 0.071 (umol N_2O m^{-2} leaf area h^{-1})	after N fertilisation and elevated root concentration respectively
rubber fig *(Ficus elastic)* , plane *(Acer platanoides)* and hazel *Corylus avellana)*	Leaves only	Bruhn et al. (2014)	0.02 to 0.05 (umol N_2O m^{-2} ground area h^{-1})	materials exposed to solar irradiance with and without UV-screening
spruce (*Picea abies*), birch (*Betula pubescens*), rowan (*Sorbus aucuparia*) and pine (*Pinus sylvestris*)	Branch measurements	Sundqvist, et al. (2012)	-0.7 (umol m^{-2} leaf area h^{-1})	Measurements on branches
ash *(Fraxinus latifolia)* cottonwood *(Populus trichocarpa)*	trees were grown in small mesocosms in greenhouse	Rice et al. (2010)	106.25 (umol CH_4 m^{-2} ground area h^{-1}) 37.5 (umol CH_4 m^{-2} ground area h^{-1})	during flooding

willow *(Salix fluviatillis)*			143.75 (umol CH_4 m^{-2} ground area h^{-1})	
European beech *(Fagus sylvatica)*, North American beech *(Fagus grandifolia)*, tulip tree (*Liriodendron tulipifera)*, red maple *(Acer rubrum) and* birch *(Betula lenta)*	upland temperate forest	Warner et al. (2017)	Up to 3.528 (umol CH_4 m^{-2} stem surface h^{-1}) (Mean 0.396 ± 0.756)	significant differences depending on tree species
tulip tree *(Liriodendron tulipifera), beech (Fagus grandifolia),* mockernut hickory *(Carya tomentosa), oaks (Quercus velutina), chestnut oak* (*Quercus michauxii),* red maple *(Acer rubrum)* and *American sweetgum (Liquidambar styraciflua)*	mature, temperate, deciduous, upland forest, USA.	Pitz and Megonigal (2017)	1.59 (umol CH_4 m^{-2} stem h^{-1}) range <-0.7 to 9.53	May-September