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Native tree species regulate nitrous oxide fluxes in tropical plantations

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Abstract. Secondary and managed plantation forests comprise a rapidly increasing portion of the humid tropical forest biome, a region that, in turn, is a major source of nitrous oxide (N2O) emissions to the atmosphere. Previous work has demonstrated reduced N2O emissions in regenerating secondary stands compared to mature forests, yet the importance of species composition in regulating N2O production in young forests remains unclear. We measured N2O fluxes beneath four native tree species planted in replicated, 21-yr-old monodominant stands in the Caribbean lowlands of Costa Rica in comparison with nearby mature forest and abandoned pasture sites at two time points (wetter and drier seasons). We found that species differed eight-fold in their production of N2O, with slower growing, late-successional species (including one legume) promoting high N2O fluxes similar to mature forest, and faster growing, early successional species maintaining low N2O fluxes similar to abandoned pasture. Across all species, N2O flux was positively correlated with soil nitrate concentration in the wetter season and with soil water-filled pore space (WFPS) in the drier season. However, the strongest predictor of N2O fluxes was fine-root growth rate, which was negatively correlated with N2O emissions at both time points. We suggest that tree-specific variation in growth habits creates differences in both N demand and soil water conditions that may exert significant control on N2O fluxes from tropical forests. With the advent of REDD+ and related strategies for fostering climate mitigation via tropical forest regrowth and plantations, we note that species-specific traits as they relate to N2O fluxes may be an important consideration in estimating overall climate benefits.

Key words: fine roots; nitrous oxide; productivity; soil nitrogen; species effects; tropical forests.

INTRODUCTION

The United Nations Framework Convention on Climate Change has identified reduced emissions from deforestation and degradation, alongside other forestry-related actions in tropical regions (REDD+), as a way to mitigate climate change (UNFCCC 2011). Not only are developing countries encouraged to slow deforestation through this program, but they may also receive financial compensation for enhancing national forest carbon (C) stocks. Some nations are currently pursuing the use of tropical tree plantations, as well as aggrading secondary forests, to accomplish these goals (Stickler et al. 2009). While carbon sequestration has been the primary focus, noncarbon environmental consequences (e.g., biodiversity effects and others) are enmeshed in this approach and are now being recognized and explicitly incorporated into REDD+ negotiations (Stickler et al. 2009, UNFCCC 2013).

One such noncarbon consideration is the production of nitrous oxide (N2O), a potent greenhouse gas with nearly 300 times the radiative forcing per molecule compared to carbon dioxide and the capacity to destroy stratospheric ozone (Forster et al. 2007). Tropical forest soils are a globally important source of N2O; estimates of annual N2O emissions from tropical forest soils range from 0.88 to 2.37 Tg N (Werner et al. 2007), second only to emissions from agriculture (Vitousek and Matson 1992, Mosier et al. 2001, Davidson 2009). These considerable fluxes are attributed to high nitrogen (N) availability relative to demand in many humid tropical forests (Vitousek and Matson 1988, Hedin et al. 2009). In ecosystems that have accumulated more N than primary producers require (i.e., N is in excess; Martinelli et al. 1999), high rates of microbial N transformations coupled with warm temperatures and high water availability can cause substantial N losses via both gaseous and hydrologic pathways (e.g., Conrad 1996, Davidson et al. 2000, Houlton et al. 2006, Brookshire et al. 2012, Koehler et al. 2012).

In the case of N2O losses, both nitrate availability and soil water-filled pore space (WFPS) regulate ultimate emissions from soils (Keller and Reiners 1994), the latter by influencing rates of gas diffusion and soil oxygen concentrations (Firestone and Davidson 1989, Perez et al. 2000). And while nitrous oxide production from the tropical biome is clearly significant in the global N2O budget, the inherent spatial and temporal variation in
controlling factors drives considerable variance in N\textsubscript{2}O emission rates across tropical landscapes. For example, differences in topographic position (Reiners et al. 1998, McSwiney et al. 2001) and substrate age or fertility status (Hall and Matson 2003) can cause nitrous oxide production rates to vary by one or two orders of magnitude, due to differences in N availability and/or soil WFPS.

Variation is also driven by human disturbances. In general, deforestation followed by forest secondary succession reduces N\textsubscript{2}O fluxes from tropical forests due to declines in N supply relative to the high demand of aggrading stands (Keller and Reiners 1994, Davidson et al. 2007). This makes aggrading forests both a carbon sink and a reduced N\textsubscript{2}O source. Some evidence suggests post-disturbance recovery of high rates of N\textsubscript{2}O eflux and a generally open N cycle with N in excess can take up to a century (Davidson et al. 2007), yet our understanding of the controls on N trace gas fluxes within aggrading stands remains limited and merits more attention as these forests continue to increase in extent and importance (Silver et al. 2000, Wright 2005, Chazdon 2008). The advent of policy metrics such as those used in REDD+ negotiations, which promote tropical forest preservation, expansion, and management as a key climate mitigation strategy (e.g., Stickler et al. 2009, Fearnside 2013, Lubowski and Rose 2013) heightens the need for this understanding, as N\textsubscript{2}O emissions can represent a notable piece of the overall climate impact of a given tropical forest stand.

Both managed and natural reforestation result in shifts in tree species composition, yet links between species shifts and N\textsubscript{2}O emissions are poorly resolved. And while natural forest regeneration following pasture and cropland abandonment is still common, an increasing fraction of the globe’s tropical secondary forests are becoming actively managed, species-specific plantations (4% of global forest area; Lugo 1997, Mayaux et al. 2005, Chazdon 2008). Tropical tree species have been shown to affect ecosystem-level C and N cycling due to differences in species traits and ecological strategies that control growth, N acquisition, and litter decomposability (e.g., Vitousek et al. 1987, Binkley and Ryan 1998, Russell et al. 2010, Russell and Raich 2012). Results to date also suggest that individual tree species may affect rates of N\textsubscript{2}O emission in both humid tropical monocultures (Erickson et al. 2002) and mature mixed forests (van Haren et al. 2007). However, comparisons of N\textsubscript{2}O fluxes in multiple monodominant stands of tropical tree species in a controlled experiment, in combination with tree trait data that allows for analysis of the driving variables, are scarce.

We investigated the effects of tree species identity on soil N\textsubscript{2}O fluxes at La Selva Biological Station (hereafter referred to as La Selva) in northeastern Costa Rica. Mature forests growing on well-drained soils in this region are known to be large emitters of N\textsubscript{2}O, with fluxes averaging 5.86 kg N\textsubscript{2}O-N-ha^{-1}yr^{-1} (Keller and Reiners 1994). Here, we used an experimental setting in which N\textsubscript{2}O fluxes from four 21-year-old monodominant plantations could be compared with adjacent abandoned pasture and mature forest. Previous work from this experimental site, wherein all planted species had similar climate, topography, parent material, and land-use history, has shown that key biogeochemical properties differ among the tree species (González and Fisher 1994, Raich et al. 2007, 2009, Russell et al. 2010). We hypothesized that differences in tree species traits would also cause interspecific differences in the production of nitrous oxide. While we assumed that all plantation plots would have lower N\textsubscript{2}O fluxes than mature forest and higher fluxes than abandoned pasture (sensu Keller and Reiners 1994, Davidson et al. 2007), we predicted that fluxes of N\textsubscript{2}O would be highest beneath species that promoted higher N availability in soil. We also predicted that species-driven differences in soil WFPS, which can emerge via traits that affect both soil bulk density and growth rates, would serve as an additional control over rates of N\textsubscript{2}O emission.

**Methods**

**Study site**

For the last three decades, annual rainfall at La Selva has averaged 4142 mm and annual temperature, 25°C (Clark et al. 2010). Precipitation delivery is seasonal, with a wetter season from approximately May to December and a drier season from approximately January to April. However, long-term rainfall averages exceed 100 mm even in drier season months. The soil has been classified as Mixed Haplic Haploperox (Kleber et al. 2007) in the Matabuey consociation (Sollins et al. 1994). This soil is relatively high in organic matter and N stocks, acidic, highly leached, and low in base saturation (Russell et al. 2007).

The experimental site was situated in a 12 ha area of La Selva that had been deforested in the mid-1950s, converted to pasture, and grazed for 30 years before abandonment in 1987. In 1988, monodominant stands of 11 tree species were planted in 50 × 50 m plots in a randomized complete block design containing four blocks (Fisher 1995, Russell et al. 2007). By 2010, four of the 11 species originally planted had survived (all native species) and are the subject of this study. The species (and Family) include: Hieronyma alchorneoides Allemão (Phyllanthaceae); Pentaclethra macroloba (Willd.) Kunth. (Fabaceae); Virola koschnyi Warb. (Myristicaceae); and Vochysia guatemalensis Donn. Sm. (Vochysiaceae). Pentaclethra is the only legume included in the experiment and is the most common overstory tree at La Selva. Whereas Hieronyma and Vochysia are typically found in the earlier successional stages, Pentaclethra and Virola become dominant as the forest matures. The understory in the plantations had been removed during the first 3–4 years of the experiment until canopy closure was reached. Thereafter, the understory was left unmanaged. By 2004, the
understory contained 255 species, but their contribution to aboveground net primary production of 20–30% did not differ significantly among tree species (Russell et al. 2010).

To provide a reference of different land cover types, four randomly selected 50 × 50 m plots within a single block (150 × 200 m) of mature forest were established in 2003 and four 14 × 6 m transects were established in an unplanted abandoned pasture in 2004. The northernmost corner of the mature forest block was situated 150 m from plantation block three, and the abandoned pasture transects, situated between plantation blocks one and four, were less than 50 m from the species plots. Both abandoned pasture and mature forest occurred on the same soil type and had the same climate as the plantations. Without true replication in these reference plots/transects, the full experimental design was classified as a randomized incomplete block.

Field and laboratory methods

Once during the wetter season (July 2010) and once during the drier season (January 2011), we measured N₂O fluxes from the 21-year-old plantations and also in the abandoned pasture and mature forest to provide end members for the study. Nitrous oxide fluxes were measured using static flux chambers (Keller and Reiners 1994, Wieder et al. 2011). On the day of sampling, 19.5 cm inner diameter PVC rings were installed in surface soils to equal depth at four randomly chosen locations within each plot, with one ring per quadrant. Surface leaf litter was removed from the ring interior and volumetric soil moisture was recorded within 5 cm of the ring using a handheld soil moisture probe inserted to 10 cm depth. We used this soil moisture measurement along with soil bulk density values to determine WFPS at the sampling time. Closed chambers, constructed from 21.3 cm inner diameter PVC end caps (headspace volume was 3.14 liters) fitted with brass bulkhead union fittings and 3.2 cm inner diameter PVC end caps (headspace volume was 3.14 liters) fitted with brass bulkhead union fittings and 3.2 cm inner diameter PVC end caps (headspace volume was 3.14 liters) fitted with brass bulkhead union fittings and 3.2 cm inner diameter PVC end caps (headspace volume was 3.14 liters) fitted with brass bulkhead union fittings and 3.2 cm inner diameter PVC end caps (headspace volume was 3.14 liters) fitted with brass bulkhead union fittings and 3.2 cm inner diameter PVC end caps (headspace volume was 3.14 liters) were placed on the rings using vacuum grease to ensure a gas-tight seal.

Gas samples (30 mL each) were collected from the chamber headspaces four times over the course of a 30-min incubation, including a time-zero sample immediately after the chamber was placed on the ring. Gas samples were stored in 20-mL serum vials that were sealed with thick butyl rubber stoppers (Bellco Glass, Vineland, New Jersey, USA). All vials were flushed with N₂ and evacuated prior to sample collection. Chamber incubations were conducted in the four species plots in each of the four blocks as well as in the mature forest plots and along the abandoned pasture transects.

Gas vials were transported to the University of Colorado where they were analyzed using a Shimadzu GC-14A gas chromatograph via an electron capture device (ECD, Shimadzu Scientific Instruments, Columbia, Maryland, USA). Rates of N₂O efflux were calculated as the linear increase in N₂O concentration in the chamber headspace over time. The few sample vials that failed to hold their gas seal (i.e., were not overpressurized) were excluded from our analyses.

In order to assess the size of inorganic N pools in soils with different plant cover types, we conducted extractions of nitrate (NO₃⁻) and ammonium (NH₄⁺) with 2 mol/L potassium chloride (KCl). We sampled soils near the N₂O static chambers twice, once in the wetter and once in the drier period. Soil samples were taken from the surface (0–15 cm) using a 3.2 cm diameter push-tube soil corer, placed in Ziploc bags, brought to the lab on ice, and processed immediately. Soil solutions with a 1:5 dry soil:KCl ratio were shaken for 30 min, allowed to settle for 30 min, and then filtered through No. 42 Whatman paper (GE Healthcare Bio-Sciences, Pittsburgh, Pennsylvania, USA). Two blanks were also extracted at every sample time to account for contaminant nitrate and ammonium in the filters and storage vials. Filtrates were kept frozen and transported on dry ice to Iowa State University where they were analyzed colorimetrically for NO₃⁻-N and NH₄⁺-N using an automated ion analyzer (QuickChem 4100, Lachat Instruments Division, Zellweger Analytics, Milwaukee, Wisconsin, USA). Field-moist subsamples of 5 g were dried at 105°C for 48 h to convert measurements to a dry-mass basis.

In January, potential net N mineralization was determined as the difference between final and initial quantities of inorganic N in fresh soil samples maintained at field moisture and incubated under aerobic conditions in the dark for seven days (Hart et al. 1994). Extractions for the final samples were conducted as indicated above. We calculated net rates of N mineralization as the difference between total inorganic N (NH₄⁺ + NO₃⁻) on day 7 and day 1.

To determine whether the tree species continued to differ in fine-root production (e.g., Russell et al. 2010), as this could affect belowground processes that regulate N₂O emissions, we measured fine-root growth in the 0–15 cm soil layer from May 2008 to May 2009 (A. Russell and J. Raich, unpublished data). We used the ingrowth core method, as described in Valverde-Barrantes et al. (2007). Measurements were conducted in all four plantation species. Fine-root growth was also measured using this technique in the mature forest in 2012–2013, thus providing a reference for that vegetation type.

Statistical analyses

Differences in N₂O emissions, inorganic N pools, and WFPS between treatments were analyzed using mixed effects models, with treatment as a fixed effect and block as a random effect. We used the Satterthwaite method for estimating the degrees of freedom for our analyses due to the incomplete nature of the block design (i.e., abandoned pasture and mature forest plots were not included in the original randomized complete block design) and restricted estimate maximum likelihood (REML) for parameter estimation within the SAS.
vegetation types (−0.5 ng N₂O-N·cm⁻²·h⁻¹) and were significantly smaller than those in Pentaclethra, Virola, and the mature forest during both sampling dates (pairwise comparisons, P ≤ 0.004 in the wetter season and P ≤ 0.005 in the drier season). Hieronyma was the next lowest N₂O-emitting species (−1.2 ng N₂O-N·cm⁻²·h⁻¹), exhibiting significantly smaller fluxes than Pentaclethra, Virola, and the mature forest during the wetter (Fig. 1) and drier (Fig. 2) sampling periods. Emissions of N₂O from the abandoned pasture (−1 ng N₂O-N·cm⁻²·h⁻¹) were most similar to Vochysia and Hieronyma, the two early successional species. Fluxes from Pentaclethra (−3.5 and 1.5 ng N₂O-N·cm⁻²·h⁻¹, wetter and drier seasons) were higher but not significantly different from the pasture in either season, yet emissions from Virola (−4 and 2 ng N₂O-N·cm⁻²·h⁻¹, wetter and drier seasons) were significantly higher than pasture in both July (Fig. 1; P = 0.038) and January (Fig. 2; P = 0.018).

During the wetter season, mean N₂O efflux was one to two orders of magnitude higher in the mature forest (−11 ± 2.5 ng N₂O-N·cm⁻²·h⁻¹) compared to the lower-emitting plantation species and abandoned pasture. However, fluxes from Virola and Pentaclethra were not statistically different from the mature forest at P = 0.05 (Fig. 1; P = 0.108 and 0.059, respectively). During the drier period, fluxes in the mature forest were greatly reduced (−1.5 ± 0.2 ng N₂O-N·cm⁻²·h⁻¹) yet were still significantly higher than Vochysia (P = 0.005) and Hieronyma (P = 0.040) and statistically similar to Virola (P = 0.218) and Pentaclethra (P = 0.792).

**RESULTS**

Nitrous oxide fluxes differed significantly among the six vegetation types in both wetter (Fig. 1; F₅,₆ = 18.31, P = 0.002) and drier (Fig. 2; F₅,₅ = 7.15, P = 0.024) seasons. Emissions from Vochysia were the lowest of all

![Graph](image-url)  
**Fig. 1.** Soil fluxes of N₂O in the wetter season from the different vegetation types, including abandoned pasture, four species in monodominant plantations (full species names in **Methods: Study site**), and mature forest. Vegetation types that share a letter are not significantly different (P > 0.05); error bars show standard errors.

![Graph](image-url)  
**Fig. 2.** Soil fluxes of N₂O in the drier season from the different vegetation types, including abandoned pasture, four species in monodominant plantations, and mature forest. Vegetation types that share a letter are not significantly different (P > 0.05); error bars show standard errors.
Soil nitrogen availability differed among the vegetation types. Extractable NO$_3^-$ concentrations were highest in the mature forest but *Pentaclethra* exhibited similarly high levels in the wetter season and was the only species with a NO$_3^-$ to NH$_4^+$ ratio greater than 1 (Table 1). Concentrations of NH$_4^+$ were similar among species in the plantations during the wet season, but during the drier period *Vochysia* and *Hieronyma* had higher ammonium concentrations than the other two species. Net N mineralization was highest in *Pentaclethra* and mature forest and lowest in *Vochysia* soils. The species also differed in WFPS, with *Pentaclethra* being the driest (July, 63%; January, 49%) and *Virola* the wettest (July, 79%; January, 64%).

In the wetter season, N$_2$O fluxes and NO$_3^-$ concentrations were positively correlated (Fig. 3a; Pearson’s $r = 0.49$, $t = 2.16$, $P = 0.048$). However, in the drier season, NO$_3^-$ did not correlate with N$_2$O emissions. Instead, WFPS was the only positively correlated soil predictor of N$_2$O fluxes in January (Fig. 3b; Pearson’s $r = 0.54$, $t = 2.28$, $P = 0.039$). Neither net N mineralization nor NH$_4^+$ concentrations correlated significantly with N$_2$O fluxes at either time point. However, fine-root growth was strongly and significantly negatively correlated with

### Table 1. Soil inorganic N concentrations and water-filled pore space (WFPS) in the different vegetation types during wetter and drier season sampling period.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Wetter</th>
<th></th>
<th></th>
<th>Drier</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NO$_3^-$ (µg/g)</td>
<td>NH$_4^+$ (µg/g)</td>
<td>WFPS (%)</td>
<td>NO$_3^-$ (µg/g)</td>
<td>NH$_4^+$ (µg/g)</td>
<td>Net N-min (µg N/g)</td>
</tr>
<tr>
<td>Pasture</td>
<td>0.72b (0.22)</td>
<td>8.41b (0.77)</td>
<td>73.0b (1.3)</td>
<td>0.27b (0.10)</td>
<td>1.69abc (0.13)</td>
<td>12.76 (9.08)</td>
</tr>
<tr>
<td>Vochysia</td>
<td>0.18a (0.09)</td>
<td>1.65a (0.40)</td>
<td>69.7b (2.2)</td>
<td>0.35b (0.15)</td>
<td>1.40a (0.33)</td>
<td>0.12a (0.39)</td>
</tr>
<tr>
<td>Hieronyma</td>
<td>0.33ab (0.12)</td>
<td>1.91b (0.37)</td>
<td>74.9b (2.4)</td>
<td>0.01a (0.003)</td>
<td>1.29b (0.28)</td>
<td>3.17b (0.46)</td>
</tr>
<tr>
<td>Pentaclethra</td>
<td>2.29b (0.34)</td>
<td>1.17b (0.36)</td>
<td>63.3b (1.4)</td>
<td>0.45b (0.10)</td>
<td>0.82b (0.28)</td>
<td>7.54b (1.30)</td>
</tr>
<tr>
<td>Virola</td>
<td>0.20ab (0.07)</td>
<td>1.51a (0.35)</td>
<td>78.9b (2.9)</td>
<td>0.02a (0.02)</td>
<td>0.24a (0.13)</td>
<td>2.61b (0.49)</td>
</tr>
<tr>
<td>Forest</td>
<td>2.98b (0.58)</td>
<td>3.80b (1.03)</td>
<td>82.4b (2.0)</td>
<td>1.12 (0.16)</td>
<td>0.66abc (0.17)</td>
<td>7.33b (2.53)</td>
</tr>
<tr>
<td></td>
<td>df 5, 5</td>
<td>6, 6</td>
<td>5, 90</td>
<td>5, 5</td>
<td>6, 6</td>
<td>90, 7</td>
</tr>
<tr>
<td></td>
<td>$F$ 31.19</td>
<td>4.66</td>
<td>10.44</td>
<td>17.41</td>
<td>5.14</td>
<td>7.49</td>
</tr>
<tr>
<td></td>
<td>$P$ 0.001</td>
<td>0.043</td>
<td>0.001</td>
<td>&lt;0.001</td>
<td>0.036</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

**Notes:** Vegetation types include abandoned pasture, four species in monodominant plantations (full species names in **Methods: Study site**), and mature forest. Values are means with SE in parentheses. Net N-min means net nitrogen mineralization over a seven day period. Test statistics from mixed effects models ($F$, $P$) are shown; vegetation types that share a letter are not significantly different ($P > 0.05$).
both wetter (Fig. 4a; Pearson’s $r = 0.76$, $t = 4.33$, $P = 0.001$) and drier (Fig. 4b; Pearson’s $r = 0.72$, $t = 3.91$, $P = 0.002$) season N$_2$O emissions.

**DISCUSSION**

In an earlier study at La Selva, Keller and Reiners (1994) observed a distinct gradient of N$_2$O, with high fluxes from mature forest soils, low fluxes from grass-dominated pastures, and intermediate fluxes from mixed, naturally regenerating secondary forest stands. While we also observed generally high fluxes in our mature forest plots at La Selva, not all aggrading forests were alike; the production of N$_2$O was dependent on the species composition of the overstory and not merely the successional stage. We propose that these significant species effects on N$_2$O emissions (eight-fold differences in wetter-season fluxes and four-fold differences in drier-season fluxes) are linked to species traits and growth habits, such as fine-root production (see Plate 1), which regulate both soil N availability and WFPS.

The two tree species in our study system that produced the most N$_2$O, *Pentaclethra* and *Virola*, are generally found in mature forests and appear to have traits that promote a more open, leaky N cycle. *Pentaclethra*, like many leguminous trees, has low litter and root C:N ratios (Raich et al. 2007, Russell et al. 2007). This species, with its N-rich tissues, low N-use efficiency, and nodulated roots, sustains high fluxes of detrital N (Russell and Raich 2012). All of these traits point to high N fluxes through the plant–soil system, during the course of which more nitrogen can be lost. This is not an altogether surprising result, as others (such as Erickson et al. 2002) have also observed elevated N$_2$O fluxes from beneath leguminous trees in monodominant tropical stands. Furthermore, while *Pentaclethra* had the highest net N mineralization rates and largest NO$_3^-$ pools (Table 1), it may have had less capacity to take up mineralized N as a result of lower relative fine-root growth (Fig. 4a and b, squares) and/or less need to take up soil N due to the capacity to fix atmospheric N$_2$. Thus, *Pentaclethra* promoted larger available N pools but was potentially a poor competitor for its uptake, leaving N pools more vulnerable to loss via N$_2$O.

Emissions from beneath *Virola* were on par with those from *Pentaclethra*, despite the fact that *Virola* did not have particularly N-rich tissues or elevated N flows within the plant–soil system (Russell and Raich 2012). However, *Virola* was among the least productive of the studied species and displayed notably low fine-root growth (Russell et al. 2010; Fig. 4a and b, diamonds). This tendency toward slow growth and low belowground biomass likely reduced its potential for acquiring N and thus lowered N uptake, rendering soil N pools more prone to transformations and losses via microbial and hydrologic pathways. Conversely, the early succes-
The lowest emitters of N$_2$O tended to be the two most productive species, none of which were legumes. Detected in that study were beneath the crowns of species associated with species differences in the production of N$_2$O, as seen in Fig. 4. Photo credit: A. E. Russell.

Our findings of potential links between N$_2$O fluxes and plant traits that determine growth rates and N demand agree with the results of Van Haren et al. (2010), who observed variation in N$_2$O fluxes beneath individual tropical trees in a diverse stand of Amazonian humid mature forest. The highest emissions of N$_2$O detected in that study were beneath the crowns of species that had low productivity, none of which were legumes. The lowest emitters of N$_2$O tended to be the two most productive species (van Haren et al. 2010), similar to our results. Importantly, the coupling between productivity and the amount of N available for N$_2$O production was not completely apparent in our study by examination of inorganic N pools alone. For instance, high N$_2$O fluxes from slow growing *Virola* were not well predicted by its low NO$_3^-$ pools (Fig. 3a, *Virola* plots above the line). In fact, a better predictor of N$_2$O fluxes in the plantations was fine-root growth rate, which scaled negatively with nitrous oxide emissions in both wet and dry periods. Consistent with correlations in the plantations, the mature forest reference plots had relatively high N$_2$O emissions and low fine-root growth, 1.46 ± 0.21 Mg C·ha$^{-1}$·yr$^{-1}$ (A. E. Russell, *unpublished data*), which was slightly less than rates in *Virola* and *Pentaclethra* of 1.91 ± 0.25 and 1.84 ± 0.31 Mg C·ha$^{-1}$·yr$^{-1}$, respectively. Thus, in order to tease out the mechanisms behind tree species effects, it seems essential to further examine processes that determine tree-specific variation in growth habits and how differences in tree N demand and N uptake affect N$_2$O emission.

Tree traits that affect soil water content may also lead to meaningful variability in N$_2$O emissions. For example, in the drier season, soil WFPS was the only positive correlate with N$_2$O fluxes (Fig. 3b), and we observed differences in soil WFPS across the three general vegetation types and between species in the plantations. Tree species traits that affect soil bulk density and water use, such as differences in organic matter inputs, root architecture, and photosynthetic demand, may thus have important implications for soil N$_2$O fluxes via effects on soil WFPS, especially during drier periods. This may help to explain why *Virola* fluxes did not decline as strongly in January as in other vegetation types (e.g., Fig. 2). *Virola'*s low belowground biomass contributed to a relatively higher soil bulk density (Russell et al. 2007, 2010), which, combined with lower growth rates, enabled WFPS in *Virola* plots to stay above 60% during the drier season (Table 1). These conditions may have continued to promote denitrification while soils beneath other species experienced hydrologic conditions unfavorable for nitrous oxide production (Davidson et al. 2000).

Our findings indicate that, through diverse mechanisms, tree species have the potential to alter the production of N$_2$O and the transition from conservative to leaky N cycling in aggrading tropical stands. Notably, those effects are not simply a product of soil N pools, but are also linked to plant traits that determine growth rates, soil water dynamics, and N uptake. Links between tree species and biogeochemical processes in tropical forests recovering from human disturbance merit attention (Silver et al. 2000, Wright 2005, Chazdon 2008), since as of 2005, half of the entire humid tropical biome had been deforested to the extent that it contained 50% or less tree cover (Asner et al. 2009). Tropical land managers and other environmental policy agents advocate the planting of trees and use of plantations to aid secondary succession and forest restoration (Lugo 1997, Rudel et al. 2005, Chazdon...
2008), with new emphasis on C sequestration as well (Stickler et al. 2009, Lubowski and Rose 2013). Because species-specific variations in N$_2$O emissions can be substantial, and given the potency of N$_2$O as a greenhouse gas, these dynamics merit consideration in restoration efforts. We suggest that in meeting REDD+ goals, an improved understanding of the influence of individual tree species on N$_2$O fluxes could (1) guide species selection in restoration and C sequestration projects, (2) aid in the design of sustainable agroecosystems that include trees, and (3) promote land-use planning for mitigation of N$_2$O emissions in a changing climate.

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