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Nitrogen release from five organic fertilizers commonly used in greenhouse organic horticulture with contrasting effects on bacterial communities

Pierre-Paul Dion, Thomas Jeanne, Mireille Thériault, Richard Hogue, Steeve Pepin, and Martine Dorais

Abstract: Organic fertilization in greenhouses relies on organic fertilizers with low carbon/nitrogen ratio. Nitrogen (N) availability thus depends on an efficient mineralization driven by microbial communities. However, data on the mineralization rate of such fertilizers are scarce, and their improper use can lead to either N deficiency, or N losses to the environment. Consequently, better knowledge of N availability following organic fertilization is crucial for the development of sustainable greenhouse organic horticulture. We investigated the effect of pelleted poultry manure (PM) and blood (BM), feather (FM), alfalfa (AM), and shrimp (SM) meals on N availability and bacterial communities in a peat-based organic growing medium and a mineral soil. Nitrogen and carbon (C) pools were measured periodically over a 52 wk incubation experiment. Bacterial communities were characterized by sequencing the regions V6–V8 of the 16S rRNA gene on the high-throughput Illumina MiSeq platform, 4 wk after the start of the incubation. Nitrogen mineralization plateaued for the mineral soil and the peat substrate at, respectively, 41% and 63% of applied N for PM, 56%–93% (BM), 54%–81% (FM), 34%–53% (AM), and 57%–73% (SM). Organic fertilizers supported markedly contrasted bacterial communities, closely linked to soil biochemical properties, especially mineral N, pH, and soluble C. Alfalfa meal promoted the highest Shannon diversity index in the mineral soil, whereas SM and PM increased it in the peat-based growing medium. Our results quantified the mineralization and highlighted the impact on bacterial communities of commonly used organic N fertilizers in conditions relevant to organic greenhouse horticulture.

Key words: bacterial diversity, greenhouse horticulture, nitrogen, organic fertilization, peat-based growing medium.

Résumé : La fertilisation biologique en serre repose sur l'usage d'engrais organiques à faible rapport carbone/azote. La quantité d'azote (N) disponible dépend d'une minéralisation efficace de cet élément par la microflore. Malheureusement, on sait peu de choses sur la minéralisation des engrais en question, ce qui en rend l'usage difficile, avec les carences en N ou les pertes de N dans l'environnement qui pourraient s'ensuivre. Pour qu'une serri-culture biologique durable voie le jour, il est donc impératif de savoir la quantité de N disponible après l'addition des engrais biologiques. Les auteurs ont étudié les effets du fumier de poules granulé (PM) et des farines de sang (BM), de plumes (FM), de luzerne (AM) et de crevettes (SM) sur la disponibilité du N et sur la population bactérienne dans un substrat tourbeux et un sol minéral. Dans cette optique, ils ont mesuré les réserves de N et de carbone (C) pendant 52 semaines. Les communautés bactériennes ont aussi été caractérisées par séquençage des régions V6-V8 du gène 16 S rRNA au moyen de la plateforme Illumina MiSeq, à la quatrième semaine d'incubation. La minéralisation de l'azote atteint un plafond dans le sol minéral et le substrat tourbeux aux taux respectifs que voici : 41 % et 63 % du N appliqué pour le PM; 56 % et 93 % pour la BM; 54 % et 81 % pour la FM; 34 % et 53 % pour

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la AM; 57 % et 73 % pour la SM. Les engrais biologiques ont permis la prolifération de communautés bactériennes très contrastantes, étroitement associées aux propriétés biochimiques du sol, principalement la concentration de N minéral, le pH et la teneur en C soluble. La farine de luzerne a donné lieu à la plus importante biodiversité (indice de Shannon) dans le sol minéral; celle de crevettes et le fumier de poules granulé ont amélioré la biodiversité dans le substrat tourbeux. Ces résultats ont permis de quantifier la minéralisation de l'azote et font ressortir l'impact des différents engrais organiques abondamment employés en serriculture biologique sur la microflore. [Traduit par la Rédaction]

Mots-clés : diversité de la microflore, serriculture, azote (disponibilité), fertilisation biologique, substrat tourbeux.

Introduction

Greenhouse organic vegetable crops can achieve high yield. They, however, require a very intensive nitrogen (N) fertilization, as N uptake can reach values as high as 1250 kg N ha⁻¹ yr⁻¹ for a yield of 50 kg m⁻² of tomatoes (Cuijpers et al. 2008; Dorais and Schwarz 2018). When planning fertilization of an organic greenhouse crop, producers and advisors currently rely mostly on recommendations intended either for soil-grown organic field crops, or conventional soilless greenhouse crops. Crops grown under organic field conditions or less intensive greenhouse systems have lower N uptake values than high-technology greenhouse crops, and plant N uptake is sustained by use of manure, compost, and cover crops (Reganold and Wachter 2016; Tittarelli et al. 2017; Zikeli et al. 2017). In conventional greenhouses, conventional inorganic fertilizers are provided through fertigation. To meet the high plant N uptake capacity of vegetables grown in intensive greenhouses, organic producers rely on organic fertilizers with a relatively high N content (low C/N ratio), often by-products from slaughterhouses, because organic amendments with higher C/N ratios, such as compost, rarely provide enough N to meet crop requirements (Burnett et al. 2016; Tittarelli et al. 2017; Zikeli et al. 2017). Indeed, fertilization that includes organic residual material depends on an efficient N mineralization rate (Myrold and Bottomley 2008; Burnett et al. 2016), as N is more easily taken up by plants in its mineral forms, nitrate and ammonium (Hawkesford et al. 2012). Moreover, even in less intensive cropping systems, the reliance on compost and manure can lead to over-abundance of phosphorus (P), as those amendments are generally imbalanced (Tittarelli et al. 2017; Möller 2018). Managing soil fertility using various organic fertilizers and amendments, with different nutrient compositions, can help maintain soil nutritive balance close to crop requirements.

Nitrogen forms are highly diversified in the soil, and up to 90% of soil N is within organic molecules and residues (Olk 2008). Pools of N-containing organic compounds are thus important sources of mineralizable N (Paul 2014), and many recent studies have demonstrated the importance of their direct uptake by the roots in the plant global N and C budget (Näsholm et al. 2009; Paungfoo-Lonhienne et al. 2012; Franklin et al. 2017; Dion et al. 2018). Finally, when C sources are abundant, a significant amount of N can be immobilized in the microbial biomass (Jones et al. 2005). It is therefore

important, in studies on N availability of organic fertilizers, to also monitor the distribution of N in its principal pools in the soil or growing medium.

Given the intricateness of the N cycle and the multiple forms of N in the soil and in the diverse types of organic amendments mixed with growing media, N fertilization management is generally based on complex models or dynamic nutrient balance models based on the total crop nutrient removal and decomposition of soil organic matter (Janssen 1984; Cuijpers et al. 2008, Voogt et al. 2011). This has led to the publication of various N management tools adapted for greenhouse management (Guo et al. 2010; Voogt et al. 2014; Gallardo et al. 2016). Furthermore, organic fertilization provides N primarily as organic matter. Hence, a key priority for the development of organic horticulture is to achieve a better knowledge of N availability following organic fertilization, for an optimal synchronization of N availability with crop N demand (Burnett et al. 2016; Tittarelli et al. 2017).

Fertilization influences the composition of microbial communities in the soil (Sun et al. 2015; Kumar et al. 2018), which in turn, influences the N cycle and availability to the plants (Isobe et al. 2018; Ma et al. 2018). Conventional inorganic fertilization alone can, over the long-term, increase microbial biomass C and N in agricultural soils (Geisseler et al. 2016; Zhang et al. 2017; Kumar et al. 2018), but the inclusion of organic matter in the form of manure, green manure, cover crops, or compost leads to a higher long-term increase of microbial biomass C and N (Six et al. 2006; Elfstrand et al. 2007; Ge et al. 2013; Zhang et al. 2017; Kumar et al. 2018). Recent developments in high-throughput sequencing platforms allowed for a much more detailed analysis of the bacterial community. Ensuing research on the effect of the soil fertilization on microbial communities has mainly focused on amendments such as compost (Mickan et al. 2018), manure (Kumar et al. 2018; Ma et al. 2018; Wolters et al. 2018), crop residues (Pitombo et al. 2016; Ma et al. 2018), and mineral fertilizers (Kumar et al. 2018; Ma et al. 2018). However, few studies have been published yet on the effects of organic fertilizers with higher N content (lower C/N ratio), such as those used in organic greenhouse horticulture, on microbial communities. Bonilla et al. (2012) reported an increased soil bacterial biodiversity following fertilization of an organically managed avocado crop with blood meal along with manure, although they did not isolate the

Table 1. Chemical composition of the five fertilizers applied in the incubation experiment.

Fertilizer	Total N (%)	NH ₄ -N (%)	C/N	Organic matter (%)	P (%)	K (%)	Ca (%)	Mg (%)
Blood meal	11.06	0.01	3.66	86.73	0.32	0.64	3.14	0.14
Feather meal	13.01	0.00	3.35	91.58	0.56	0.17	1.03	0.05
Alfalfa meal	2.59	0.11	15.86	89.32	0.22	2.68	1.57	0.27
Shrimp meal	5.69	0.01	4.74	58.18	4.75	0.10	11.84	0.86
Pelleted poultry manure	5.19	0.17	6.30	70.37	1.35	2.29	6.83	0.44

Note: Analyses were performed by AgriQuanta Inc., St-Ours, QC, Canada. N, nitrogen; C, carbon; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium.

effect of blood meal from the manure effect (i.e., with manure only or blood meal only treatment). Gravel et al. (2012) reported an increased microbial activity as measured by fluorescein diacetate hydrolysis, but a slightly reduced CO₂ flux after the application of shrimp meal to sweet pepper transplants grown in a peat-based growing medium.

In our study, five fertilizers were investigated on the basis of their market availability, low C/N ratio, and usage by the local (province of Québec, Canada) and worldwide organic greenhouse industry: blood meal (BM), feather meal (FM), pelleted poultry manure (PM), shrimp meal (SM), and alfalfa meal (AM). Their C/N ratios and contents in N, P, potassium (K), magnesium (Mg), calcium (Ca), and organic matter are presented in Table 1. Blood meal and FM have been reported to provide a fast and high-percentage N mineralization (Agehara and Warncke 2005; Hammermeister et al. 2006; Hartz and Johnstone 2006; Gaskell and Smith 2007; Sullivan et al. 2010). Pelleted poultry manure is considered in the literature as a slow-release N fertilizer (Hartz et al. 2000; Gaskell and Smith 2007), yet producers in Canada tend to use it as a fast-release organic N amendment (Weill and Duval 2009). Alfalfa meal is reported to be a slow-release N fertilizer (Agehara and Warncke 2005; Hammermeister et al. 2006; Sullivan et al. 2010), which is consistent with its higher C/N ratio. To our knowledge, no N mineralization data have been published on SM, which have been, hitherto, mainly studied for swine nutrition (Fanimio et al. 2006). Øvsthus et al. (2015) nevertheless reported a “potentially plant-available N based on mineralization from incubation (unpublished data)” of 54.1% for dried shrimp shells. Shrimp meal has also shown good potential in its use as an organic fertilizer for vegetable crops (Gravel et al. 2012; Øvsthus et al. 2017). All mineralization experiments involving organic fertilizers reported earlier were performed in mineral soils, and, to our knowledge, there has been no such incubation performed using organic growing media.

Through a 364 d incubation experiment, we investigated the mineralization rate evolution of five different organic fertilizers, and the distribution of N in different pools in a mineral soil and in a peat-based organic growing medium, along with the effects on the C pools. We

thus provide data on plant-available N from common organic fertilizers and contrasted soil or growing medium biochemical effects among those fertilizers.

We hypothesized that organic fertilizers with different chemical compositions would influence bacterial diversity and, consequently, the release of mineral N. More precisely, we hypothesized that fertilizers providing a balanced nutrient composition or a higher quantity of easily degradable C would support a higher bacterial diversity and activity, a greater N immobilization in microbial biomass and, thus, a slower N mineralization.

Materials and Methods

Soils

A mineral soil and a peat-based growing medium were compared in this incubation study. The mineral soil had been under organic greenhouse production for the previous 35 yr and was sampled at Les Serres Pleine Terre (St-Joseph-de-Beauce, QC, Canada). It is a Bullard loamy sand, orthic gleysol with 14.8% organic matter content. Previous fertilization management of the soil included feather meal, pelleted poultry manure and composted crop residues. The peat-based organic growing medium (Fafard, St-Bonaventure, QC, Canada) contains compost, perlite, coco fiber, and clay (undisclosed proportions) with an organic matter content of 75.0%. It was sampled in our experimental greenhouses (Laval University, Québec, QC, Canada) after an organic cucumber crop. Previous N fertilization management included applications of blood meal, feather meal, shrimp meal, and pelleted poultry manure, along with compost (Fertilo® Composted Chicken Manure with Sphagnum Peat Moss and Biofor® Compost with Peat and Bark, Fafard, St-Bonaventure, QC, Canada). Both soil and growing medium were air-dried at 30 °C prior to the incubation experiment. Initial physical and biochemical properties of the mineral soil and the peat-based growing medium are summarized in Table 2. The mineral soil was sieved at 4 mm. The organic growing medium was not sieved because it would have also removed porous particles (e.g., perlite); larger particles (>4 mm) such as woody debris were, however, removed by hand.

Table 2. Initial biochemical and physical properties of the mineral soil and organic growing medium used in the incubation.

	Mineral soil	Organic growing medium
Sand (% of mineral fraction)	80	—
Silt (% of mineral fraction)	18	—
Clay (% of mineral fraction)	2	—
Organic matter (%)	14.8	75.0
Bulk density in situ (g cm^{-3} dry soil) ^{a,b}	0.71 ^c	0.11
Bulk density in jar (g cm^{-3} dry soil) ^b	0.45	0.11
Gravimetric water content (g g^{-1})	0.40	0.73
Total C (% dry soil)	10.2	37.6
Total N (% dry soil)	1.03	1.87
N _{min} (mg N kg^{-1} dry soil)	586.3	272.7
Microbial biomass C (mg C kg^{-1} dry soil)	140.5	798.0
Microbial biomass N (mg N kg^{-1} dry soil)	27.9	106.7
Soluble organic N (mg N kg^{-1} dry soil)	27.4	149.8
Soluble organic C (mg C kg^{-1} dry soil)	117.9	352.2
pH (in 2:1 water extract)	5.42	6.21
EC (mS cm^{-1} in 2:1 water extract)	2.95	0.92

Note: When not stated otherwise, values are for the substrate in the jar at the start of the incubation. C, carbon; N, nitrogen; EC, electrical conductivity.

^aIn situ bulk density was determined using samples collected between 4 and 10 cm depth in the greenhouse.

^bSoil and growing medium used for bulk density calculation were weighed after drying at 105 °C.

^cLow density of the mineral soil is explained by soil labor and frequent and abundant compost addition.

Incubation experiment

An in vitro static aerobic incubation was performed for a duration of 52 wk, in a growth chamber maintained in the dark, at 21 °C and 90% air relative humidity. Although in vitro static aerobic incubations do not account for N uptake by the plant (Canali et al. 2011) or for the enhancement of N mineralization by root exudates (Badri and Vivanco 2009; Zhu et al. 2014), they allow re-immobilization of mineralized N by the microorganisms that usually compete with the plants (Pansu and Thuriès 2003). In 500 mL mason jars, 80 g of air-dried mineral soil or 40 g of air-dried growing media were weighed. Watering was performed 10 d before fertilizer addition to let stabilize the microbial activity and re-immobilize the C and N that were released following drying (Van Kessel et al. 2000; Butterly et al. 2010; Yu et al. 2014). Demineralized water was added to the soil at a gravimetric water content of 40% in the mineral soil and 73% in the organic growing medium. Water content was adjusted each second week and the week before each sampling by weighing the jar and adding water to a constant mass. Additionally, a 5-mm-diameter hole was punched in each jar lid to maintain aerobic conditions.

The amount of N to incorporate in each incubation treatment was calculated to simulate the fertilization needed to meet N requirements of a greenhouse cucumber crop for 1 mo. Recommended N fertilization in conventional cucumber greenhouse crops varies

depending on the reference, from 9 (fertilization in artificial, non-organic growing medium; OMAFRA 2010) to 14 g N plant⁻¹ mo⁻¹ (surface application on a mineral soil; Papadopoulos 1994). Nitrogen uptake data from Voogt et al. (2014) indicate ca. 10 g N plant⁻¹ mo⁻¹ in an organic tomato crop grown in a mineral soil. In a cucumber greenhouse experiment fertilized with blood meal and feather meal, we monitored 12.8 g N plant⁻¹ mo⁻¹ (unpublished data). We thus calculated the fertilizer application F_a to an equivalent of 11 g N plant⁻¹ mo⁻¹. In the mineral soil, considering a dry bulk density ρ_{min} of 0.71 g cm⁻³, an effective rooting depth r of 0.2 m, a planting density D of 1.8 plants m⁻² (total greenhouse area basis) and a fertilizer application concentrated along the base of plant shoots (33% of greenhouse area), we determined the fertilizer application F_{min} as 0.44 g N kg⁻¹ dry mineral soil.

$$F_{\text{min}} = \frac{F_a \times D}{r \times \rho_{\text{min}} \times 0.33 \times 1000}$$

In the peat-based growing medium, considering a dry bulk density ρ_{org} of 0.11 g cm⁻³ and a growing medium volume V of 70 L m⁻² greenhouse area (Canadian organic standard reduced the volume from 70 to 60 L m⁻² in March 2018, see Government of Canada 2015), fertilizer application F_{org} was 2.54 g N kg⁻¹ dry growing medium.

$$F_{\text{org}} = \frac{F_a \times D}{V \times \rho_{\text{org}}}$$

Table 3. Amount of fertilizers in the six fertilization treatments for the two incubated soils.

Fertilizer	Mineral soil		Peat-based growing medium	
	g fertilizer kg ⁻¹ dry soil ^a	g N kg ⁻¹ dry soil ^b	g fertilizer kg ⁻¹ dry medium ^a	g N kg ⁻¹ dry medium ^b
Blood meal	3.65	0.40	21.18	2.34
Feather meal	3.36	0.44	19.55	2.54
Alfalfa meal	14.58	0.38	127.05	3.29
Shrimp meal	6.73	0.38	39.09	2.22
Pelleted poultry manure	8.75	0.45	50.82	2.64
Control	0	0	0	0

^aCalculations for fertilizer application based on product label.

^bValues of nitrogen (N) content in each fertilizer are based on chemical analysis results (Table 1).

The five aforementioned fertilizers (BM, FM, AM, SM, and PM) commonly used by organic growers were incubated individually, along with an unfertilized control. All calculations for fertilizer application were based on the N content reported on each fertilizer label, whereas data analysis was performed using the real chemical composition of each fertilizer as determined by a certified laboratory (Table 1). Resulting fertilizer applications are presented in Table 3.

The first week (thereafter referred to as week 0) was set on 10 Aug. 2015 for the growing medium and on 12 Oct. 2015 for the mineral soil. The fertilization was performed on the first day of week 0 by applying each fertilizer to all corresponding jars just before gas sampling and by mixing soils manually using a spatula. Gas samples were collected on day 1 of each sampling week. The sampled jars were refrigerated at 4 °C on day 2 for the rest of the week, during which the extractions were performed. Each treatment was replicated four times. There were thus 432 jars incubated (two soils × six fertilizers × nine sampling times × four replicates). Destructive soil samplings were performed on weeks 0, 1, 2, 4, 9, 18, 27, 39, and 52 by randomly selecting four jars per treatment (i.e., fertilizer × soil type).

Soil measurements

Gas sampling

Gas sampling was performed over a 24 h period using the nonsteady-state chamber method as described in Rochette and Bertrand (2007). At time 0, the pierced jar lid was replaced by an airtight cap with a septum designed to receive the needle for the gas sampling, and a valve through which pure helium was added to equilibrate gas pressure without altering the relative concentration of the gas of interest. Gas samples were collected after 30 min, 6 h, and 24 h. CO₂, CH₄, and N₂O concentrations were assessed using a gas chromatograph 450-GC (Bruker Corporation, Billerica, MA, USA).

Soil extractions

Soluble ions were extracted by adding 20 mL of distilled water to 10 g of fresh soil or growing medium,

and their concentration was determined by ion chromatography in an ICS-2100 (Dionex Corporation, Sunnyvale, CA, USA) for the anions (NO₃⁻, NO₂⁻, PO₄³⁻, and SO₄²⁻) and in an ICS-1100 (Dionex Corporation, Sunnyvale, CA, USA) for the cations (NH₄⁺, K⁺, Mg²⁺, and Ca²⁺). The same water extract was used to measure pH and electrical conductivity (EC) with an Accumet XL-500 dual pH and conductivity meter (Thermo Fisher Scientific, Waltham, MA, USA). Extractable ammonium (NH₄⁺) and nitrate (NO₃⁻) were extracted with KCl 2 mol L⁻¹ and dosed in a colorimeter QuickChem 8500 serie II (Lachat Instruments, Loveland, CO, USA) (Maynard and Kalra 2007). Total soluble C and N were extracted according to Chantigny et al. (2007), using a 5 mmol L⁻¹ CaCl₂ extraction solution for the mineral soil, and water for the organic soil. The soluble organic N (SON) was then calculated by subtracting soluble NO₃⁻ and NH₄⁺ from the total soluble N. As inorganic C (i.e., carbonates) levels were below the detection limit, soluble organic C (SOC) was considered as equal to the total soluble C. Microbial biomass C and N were determined by extraction with K₂SO₄ (Croft et al. 2001) before and after soil fumigation with chloroform (Voroney et al. 2007). Total C and N in the extracts for total soluble C and N and microbial biomass C and N were determined using a TOC-V analyzer coupled with a TNM-I (Shimadzu Corporation, Tokyo, Japan). Soil gravimetric water content was determined by weight loss after drying for 24 h at 105 °C. Total N and C in the soil were determined on air-dried soil samples using an automated Leco CNS-2000 dry combustion analyzer (Leco Corporation, St-Joseph, MI, USA).

Bacterial diversity

An amount of 0.5 g of each soil or growing medium from week 4, air-dried, was used for DNA extraction. There were thus four replicates per treatment. We used the commercial FastDNA Spin Kit for soil (MP Biomedicals, Solon, OH, USA) coupled with a FastPrep®-24 (MP Biomedicals, Solon, OH, USA) homogenization step following the manufacturer's instructions. DNA was stored at -20 °C until further analysis. The amplification of the bacterial 16S rRNA gene was

done as previously described by Comeau et al. (2017). The library preparation was completed using a dual-indexed polymerase chain reaction approach specifically designed for Illumina instruments by the genomic analysis platform at the Institut de biologie intégrative des systèmes (IBIS, Laval University, Quebec, QC, Canada). The samples were sequenced on an Illumina MiSeq instrument using a 2×300 bp sequencing kit.

Raw sequences were processed as described in Brassard et al. (2018). Briefly, forward and reverse fragments were joined under QIIME version 1.9.1 (Caporaso et al. 2010) using the fastjoin tools. An open reference approach was used with the reference database SILVA version 119 (Quast et al. 2012) to produce the operational taxonomic unit (OTUs) tables. OTU tables were standardized to 7000 sequences per sample before computing richness diversity and comparative matrices.

Statistical analyses

Statistical analyses were performed using R version 3.5.0 (R Core Team 2018) with packages lme4 version 1.1-14 (for non-linear regression), aod version 1.3 (for Wald test), agricolae version 1.2-8 (for least significant difference test), and vegan version 2.5-2 [for nonmetric multidimensional scaling (NMDS) and Adonis test].

The total CO_2 -C efflux for a whole year equivalent of the incubation was calculated as the area under the curve (AUC) of the evolution of the CO_2 flux along the experiment period of time. Using a Bootstrap procedure, we randomly selected the flux from one sample from each fertilizer at each sampling time (i.e., nine samples for each fertilizer) and calculated the AUC with the trapezoid method. This random selection was repeated 1000 times. The mean AUC values were compared among treatments using the Wald test, adjusted according to the Benjamini–Hocheberg procedure with $Q = 0.05$.

Dispersion of the bacterial populations was analyzed by NMDS based on the Bray–Curtis distance matrix of the bacterial OTUs (Beals 1984). The soil biochemical parameters, among those presented in Table 4, which were significantly linked to the composition of the bacterial community (test resulting from Adonis procedure, i.e., permutational multivariate analysis of variance, using the *adonis2* function from package *vegan* in R) were fitted on the NMDS ordination (function *envfit* from package *vegan*, see Borcard et al. 2011). Mineral N, microbial biomass C and N, and soluble organic C and N were linked to the bacterial community data both as their value at week 4 and as the value of their variation (slope) from weeks 0 to 4. Gas fluxes (CO_2 , CH_4 , and N_2O) were linked together both as the flux at week 4 and the total efflux between weeks 0 and 4.

Results

Chemical analyses

In general, the N mineralization of the control and of the 10 combinations (two substrates \times five fertilizers)

followed different patterns over time, with clear differences between the mineral soil and the peat-based growing medium (see curves in Figs. 1A and 1B and corresponding equations in Table 5). Mineralization started to plateau for both types of soil and all studied fertilizer treatments after ca. 60 d only (Fig. 1). Alfalfa meal caused a net N immobilization in the first week and achieved the lowest total N mineralization of all fertilizers. In the mineral soil, PM reached a higher, but not significantly different N mineralization relative to AM, whereas SM, BM, and FM achieved a similar maximum mineralization. In the growing medium, the fertilizers, ordered from the lowest to the highest total mineralization, were AM, PM, SM, FM, and BM. Pelleted poultry manure released the highest initial extractable mineral N at week 0: 20.1% of applied N in the mineral soil and 33.4% of applied N in the growing medium. However, the mineralization rate of PM (related to parameter *b* in the equations; Table 5) was the lowest in the growing medium and intermediate in the mineral soil thereafter.

All fertilizers induced an initial CO_2 (Figs. 2A and 2B) and N_2O (Figs. 5P and 5V) flux higher than the control. However, the high initial value of CO_2 flux observed in the growing medium rapidly decreased to reach levels below that of the control, resulting in an annual CO_2 efflux significantly lower than the control for all fertilizers, except AM (Fig. 2D). Following AM application, the N_2O flux was 13.5 and 9.5 times higher in, respectively, the peat-based growing medium (Fig. 5P) and the mineral soil (Fig. 5V) than the highest recorded flux for any other fertilizer. This flux rapidly declined thereafter, reaching values similar to the control from week 9 onward. Blood meal, FM, and PM had their highest N_2O flux after 1 wk, which then also declined to values similar to that of the control. From week 1 onward, SM application led to the lowest N_2O flux among the tested fertilizers.

Alfalfa meal yielded the highest initial soluble organic C, CO_2 flux, total CO_2 efflux for the whole incubation period, and microbial biomass C in both soils (Figs. 2–4). Blood meal and SM also significantly increased the initial microbial biomass relative to the control in the mineral soil, while this positive effect in the growing medium was not significant (Figs. 3A and 3B). After 9 wk in the mineral soil and 4 wk in the growing medium, the microbial C was at levels similar to or below that of the control for all fertilizers except AM. Meanwhile, there was a depletion of soluble organic C, which was more apparent in the growing medium (Fig. 4B) than in the mineral soil (Fig. 4A). Furthermore, in the growing medium, the soluble organic C in the unfertilized control steadily increased throughout the incubation, to attain values higher than that of other fertilizers. Under the control treatment in the mineral soil, the soluble organic C was lower than for all fertilizers.

Results of the microbial N and the SON were not as clear as the corresponding C values. The relatively high

Table 4. Adonis test of the relationship between bacterial community and soil chemical parameters after 4 wk of incubation.

	Mineral soil		Peat-based growing medium	
	R^2	P^a	R^2	P^a
Treatment				
Fertilizer effect	0.49	0.001	0.66	0.001
N and C pools at week 4				
N _{min} (KCl extract)	0.11	0.009	0.23	0.002
Microbial biomass C	0.13	0.005	0.23	0.002
Microbial biomass N	0.04	0.802	0.03	0.845
Soluble organic C	0.06	0.192	0.26	0.002
Soluble organic N	0.04	0.823	0.24	0.002
Total soluble N	0.12	0.005	0.26	0.002
Slope along weeks 0–4, N and C pools				
N _{min} (KCl extract)	0.10	0.006	0.17	0.005
Microbial biomass C	0.10	0.009	0.06	0.209
Microbial biomass N	0.05	0.288	0.08	0.077
Soluble organic C	0.15	0.005	0.22	0.002
Soluble organic N	0.08	0.022	0.22	0.002
2:1 water extract at week 4				
PO ₄ ³⁻	0.08	0.032	0.14	0.006
K ⁺	0.12	0.006	0.19	0.004
Mg ²⁺	0.10	0.009	0.28	0.002
Ca ²⁺	0.13	0.004	0.30	0.002
SO ₄ ²⁻	0.04	0.700	0.15	0.005
EC	0.03	0.911	0.23	0.002
pH	0.09	0.015	0.28	0.002
Gas flux at week 4				
CO ₂	0.12	0.005	0.30	0.002
CH ₄	0.06	0.168	0.12	0.017
N ₂ O	0.06	0.104	0.09	0.045
Total gas efflux in weeks 0–4				
CO ₂	0.14	0.005	0.24	0.002
CH ₄	0.07	0.146	0.26	0.002
N ₂ O	0.13	0.006	0.20	0.002
M-III micronutrients at week 4				
Fe	0.03	0.996	0.14	0.007
Mn	0.07	0.044	0.11	0.024
Zn	0.03	0.980	0.04	0.538
Cu	0.03	0.911	0.07	<i>0.096</i>

Note: C, carbon; N, nitrogen; EC, electrical conductivity; Fe, iron; Mn, manganese; Zn, zinc; Cu, copper.

^a P values corrected by the Benjamini–Hochberg (false discovery rate) method. Bold P values indicate a significant relationship ($P < 0.05$) and italic values indicate a nonsignificant tendency ($0.05 < P < 0.1$).

level of noise around total N values in the extractions, resulting from the very high concentration of inorganic N, may have caused the confounding variability observed in Figs. 3C–3D and 4C–4D. However, our results suggest that AM maintained a higher N immobilization in microbial biomass through most of the incubation, whereas PM maintained the lowest microbial N (Figs. 3C–3D). Soluble organic N was lower for the control, especially in the growing medium. Among

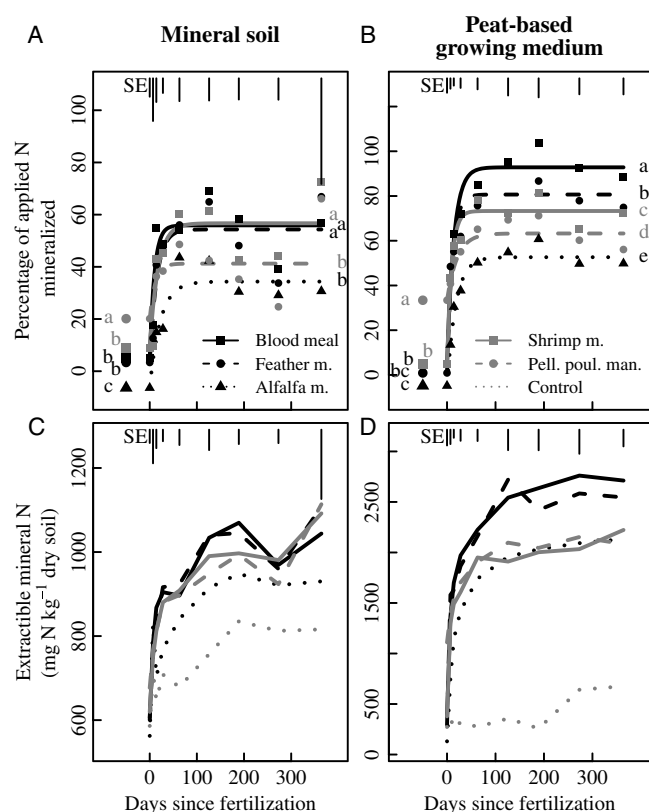
fertilizers, PM released the highest initial SON in both the mineral soil and growing medium, whereas BM and FM released the lowest (along with SM in the growing medium).

Bacterial community

The bacterial community was highly contrasted among the different fertilizers applied in mineral soil and in growing medium (Figs. 6 and 7). Shannon index

Fig. 1. Nitrogen mineralization curves following fertilizer application (A and B), calculated from the extractable nitrate and ammonium difference between a given fertilizer and the unfertilized control (C and D). The equations are presented in Table 5. Letters on the right side of the curves in (A) and (B) compare the asymptote from the curve ($y_0 + a$), i.e., the maximum mineralization.

Asymptotes with a same letter are not significantly different from each other according to the Wald test ($\alpha = 0.05$, adjusted according to the Benjamini–Hochberg procedure with $Q = 0.05$). Data points on the left side of the figure in (A) and (B) represent the immediate mineralization (or immobilization in the case of alfalfa meal) at week 0. Data points with a same letter are not significantly different from each other according to the least significant difference test ($\alpha = 0.05$). Data points along the curves indicate the means for each fertilizer (or control) at each sampling time.



takes into account both richness (number of observed species) and evenness (distribution of effectives among species) in the assessment of biodiversity, whereas the Chao index estimates real species number from the observed richness (Kim et al. 2017). In the mineral soil, application of AM resulted in the highest bacterial alpha diversity according to the Shannon index, whereas BM decreased the Shannon index compared with the control (Fig. 6A). In the growing medium, SM and PM increased the bacterial alpha diversity expressed by the Shannon index compared with the other treatments, whereas FM decreased it. In the mineral soil, AM and PM increased the richness (as described by the Chao index), whereas

BM and FM decreased it (Fig. 6C). All fertilizers except AM significantly increased the Chao index in the organic growing medium, with PM leading to the highest increase (Fig. 6D). The NMDS ordination shows a clear clustering among the fertilizers applied (Fig. 7). In only two cases, the bacterial communities did not vary greatly among treatments: in the mineral soil, application of PM did not modify the composition of the bacterial community relatively to the control; in the growing medium, FM and BM also appeared to support similar bacterial community compositions (Fig. 7B), despite having a different Shannon richness index (Fig. 6B).

The type of fertilizer and the biochemical properties that they provided to the soil or growing medium had a sharp effect on the composition of bacterial communities, as indicated by the results of the overall Adonis test (mineral soil: $R^2 = 0.49$, $P = 0.001$; peat-based growing medium: $R^2 = 0.66$, $P = 0.001$; Table 4). In the mineral soil, the following biochemical parameters significantly influenced microbial communities measured at week 4: mineral N, microbial C, total soluble N, soluble PO_4^{3-} , K^+ , Mg^{2+} and Ca^{2+} , pH, CO_2 flux, and Mn. From weeks 0 to 4, mineral N, microbial C, soluble organic C and N increases, the total CO_2 , and N_2O effluxes significantly affected the soil microbial communities (Table 4). In the organic peat-based growing medium, all chemical parameters, except microbial N at week 4, microbial C and N variation from weeks 0 to 4 and M-III Zn and Cu, had a significant relationship with the growing medium bacterial composition. The chemical variables significantly related to bacterial communities were fitted to the NMDS (Fig. 7). As several variables were closely linked to one another, the following parameters were not shown in Fig. 7 to improve its clarity: EC, SON, and mineral N were closely related to total soluble N; soluble organic C and microbial C were linked to CO_2 flux at week 4; Mg^{2+} was linked to Ca^{2+} ; SO_4^{2-} was related to PO_4^{3-} .

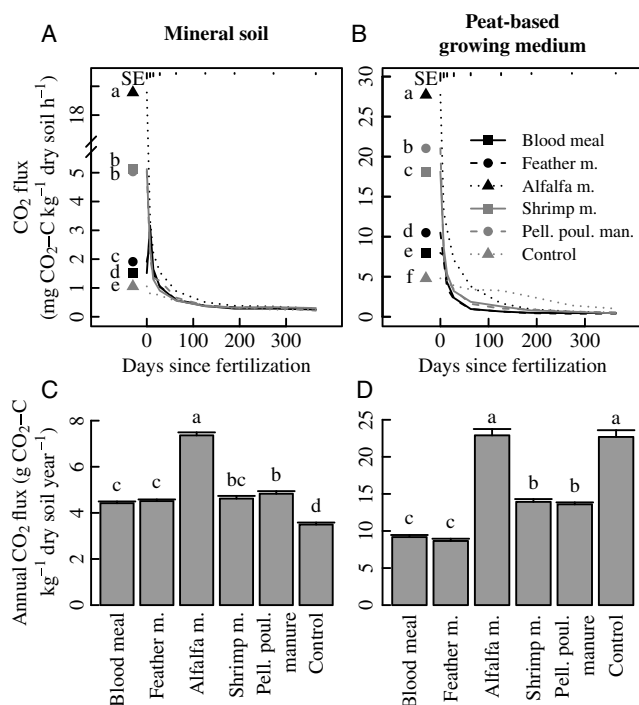
In the mineral soil (Fig. 7A), AM was associated with the highest soluble organic C, microbial biomass C and CO_2 and N_2O fluxes, and the lowest total soluble N, and the steepest soluble organic C decline in the first 4 wk. Blood meal, SM, and FM liberated more total soluble N at week 4 (faster release of mineral N) and had a slower decline in microbial C, whereas SM provided the highest amount of soluble phosphate and sulfate. pH of the water extract was highest in the mineral soil fertilized with AM, and lowest after the application of BM. The 13 fitted soil parameters (CO_2 flux, total CO_2 efflux from weeks 0 to 4, microbial C slope from weeks 0 to 4, soluble K^+ and Ca^{2+} , total N_2O efflux from weeks 0 to 4, mineral N slope from weeks 0 to 4, pH, soluble PO_4^{3-} , soluble organic C and N slopes from weeks 0 to 4, total soluble N, and M-III Mn) accounted for 74.0% of the variation observed in bacterial communities in the mineral soil, according to the Adonis test ($R^2 = 0.740$, $P = 0.001$). In the peat-based growing medium (Fig. 7B), AM was associated

Table 5. Parameters of the equations^a for mineralization curves presented in Fig. 1.

Fertilizer	Mineral soil			Peat-based growing medium		
	y_0	a	b	y_0	a	b
Blood meal	5.00 (0.85)	50.90 (3.32)	0.101 (0.034)	4.82 (3.53)	88.00 (1.91)	0.071 (0.007)
Feather meal	3.35 (2.25)	50.98 (3.39)	0.067 (0.020)	0.90 (2.31)	79.75 (1.82)	0.093 (0.010)
Alfalfa meal	-6.39 (3.29)	40.73 (3.84)	0.044 (0.018)	-4.86 (0.92)	57.50 (1.92)	0.055 (0.008)
Shrimp meal	8.76 (1.67)	47.93 (3.56)	0.057 (0.018)	4.93 (3.41)	68.37 (1.78)	0.106 (0.014)
Pelleted poultry manure	20.14 (5.12)	21.09 (3.41)	0.086 (0.082)	33.40 (5.54)	29.85 (1.96)	0.048 (0.013)

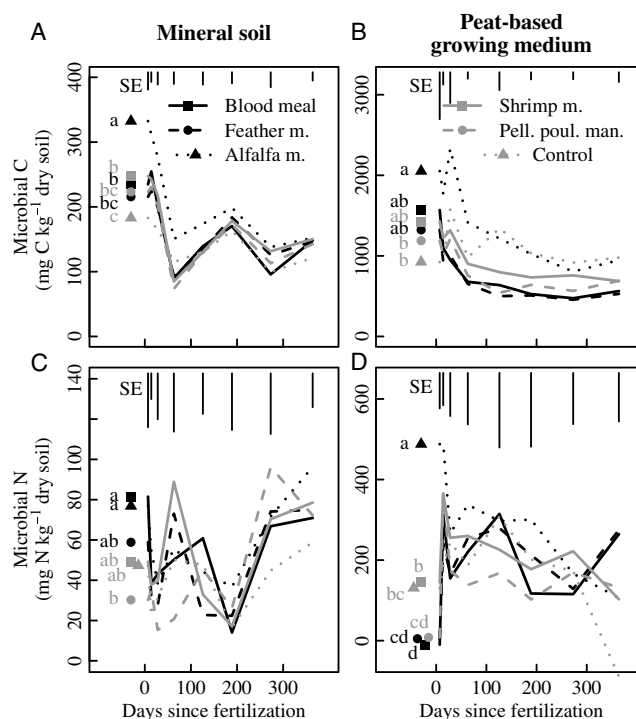
^aEquations follow the form $fN_{\min} = y_0 + a(1 - e^{-bt})$, where fN_{\min} is the percentage of applied N mineralized after t days. Standard errors are in parentheses.

Fig. 2. The CO₂ flux of the incubated soils. (A) and (B) present the evolution of the CO₂-C flux through the whole duration of the incubation for, respectively, the mineral soil and the peat-based growing medium. Data points indicate the flux at week 0, and those accompanied by a same letter are not significantly different according to the least significant difference test ($\alpha = 0.05$). (C) and (D) present the total CO₂-C efflux during the year of the incubation, calculated as the area under the curves in (A) and (B) (mean area under the curve \pm standard deviation). Treatments with a same letter are not significantly different from each other according to the Wald test after the Bootstrap procedure ($\alpha = 0.05$, adjusted according to the Benjamini–Hochberg procedure with $Q = 0.05$).



with highest CO₂ and N₂O but lowest CH₄ fluxes. The control had the lowest total soluble N and Ca²⁺ and highest pH values. Blood meal and FM caused a higher CH₄ efflux in the first 4 wk and provided more soluble Ca²⁺ and N, in addition to a faster increase in SON than other fertilizers. Pelleted poultry manure had a higher N₂O flux, whereas SM had a higher pH, closer to the control.

Fig. 3. Temporal evolution of microbial carbon (C) (A and B) and nitrogen (N) (C and D) in the mineral soil (A and C) and peat-based growing medium (B and D) during the incubation. Data points indicate the microbial C or N at week 1. Data points with a same letter are not significantly different according to the least significant difference test ($\alpha = 0.05$).

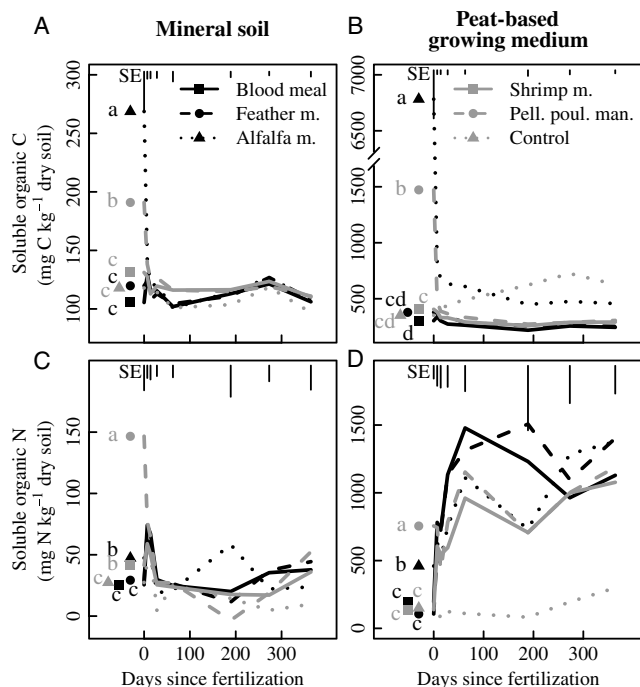


The 16 fitted soil parameters (Ca²⁺, CH₄ flux, total CH₄ efflux from weeks 0 to 4, CO₂ flux, total CO₂ efflux from weeks 0 to 4, M-III Fe, K⁺, M-III Mn, N₂O flux, total N₂O efflux from weeks 0 to 4, pH, PO₄³⁻, soluble organic C slope from weeks 0 to 4, SON slope from weeks 0 to 4, and total soluble N) accounted for 86.9% of the variation observed in bacterial communities in the growing medium, according to the Adonis test ($R^2 = 0.869$, $P = 0.001$).

Discussion

The five studied organic fertilizers provided very contrasting effects on the soil biochemical and microbial

Fig. 4. Temporal evolution of the concentration of soluble organic carbon (C) (A and B) and nitrogen (N) (C and D) in the mineral soil (A and C) and the peat-based growing medium (B and D). Data points indicate the soluble organic C or N at week 0. Data points with a same letter are not significantly different according to the least significant difference test ($\alpha = 0.05$).



properties. To our knowledge, this is the first incubation study on the mineralization of organic fertilizers in a peat-based organic growing medium.

In concordance with our hypothesis, each organic fertilizer supported contrasting bacterial communities and provided a distinct N mineralization rate, depending mostly on their C/N ratio and biochemical composition in nutrients other than N. Blood and feather meals provided a fast and almost complete mineralization of their N, especially in the peat-based growing medium. This was expected due to their low C/N ratio (Joseph et al. 2017) and is in accordance with mineralization rates previously reported in mineral soils (Agehara and Warncke 2005; Hammermeister et al. 2006; Hartz and Johnstone 2006; Gaskell and Smith 2007; Sullivan et al. 2010). However, for a given amount of N applied, when compared with the other fertilizers, BM and FM treatments led to a lower SOC, microbial biomass C, and cumulative CO₂ efflux. Considering also the lowest bacterial alpha diversity and richness observed in these two fertilizers, BM and FM provided conditions that are less than optimal for bacteria, particularly in the mineral soil, in which microbial activity appears to be limited by C availability. Moreover, they contain mostly N and very little P and K, making them unbalanced fertilizers relative to crop nutrient requirements (Möller 2018).

A balanced fertilization contributes to achieving optimal crop growth (Parent et al. 2013) and is also important for sustaining the stoichiometry homeostasis of microbial communities (Xu et al. 2015). Blood and feather meals should thus only be used in combination with other organic fertilizers or amendments, to which they can efficiently supplement N deficiencies.

Shrimp meal and PM supported a more diverse and abundant bacterial community by providing a more balanced mineral input to the soil with P, Ca²⁺, and Mg²⁺, along with a higher C/N ratio relatively to BM and FM (Xu et al. 2015). This was the case especially in the peat-based growing medium, where the high availability of soluble C supported a higher microbial biomass, potentially limited by nutrient availability. In P-limited crops, meeting crop P demand using organic fertilizers such as SM and PM could be a good alternative to mineral sources of P, which can have negative effects on phosphate-solubilizing bacteria (Mander et al. 2012; Ikoyi et al. 2018; Möller et al. 2018). Future research on N availability should, however, also study organic fertilizers with high P content to integrate organic fertilization management on multiple nutrients. Furthermore, PM supplies an immediate mineral N release at the time of application, which can be useful for quickly resolving N deficiencies. This can explain the contradiction reported in introduction (slow mineralization reported in the literature, yet used as a high N availability fertilizer by the industry in Quebec): PM indeed supports a slow mineralization but nevertheless provides a significant flush of mineral N immediately at application time (Table 5 and Fig. 1).

Alfalfa meal sustained microbial biomass and activity by providing a higher initial quantity of soluble organic C, at the expense of a reduced mineralization, as expected due to its high C/N ratio. In that way, AM appears to behave intermediately among the other organic fertilizers tested, which released N quite rapidly, and other organic amendments such as manure or compost, that have a low N concentration, i.e., a high C/N ratio, and thus release little N but stimulate the microbial activity (Paul 2014; Congreves and Van Eerd 2015). Alfalfa meal also contributed to the highest emission of N₂O among tested fertilizers, probably resulting from a higher bacterial nitrifying and denitrifying activity sustained by soluble organic C availability (Graham et al. 2017). Stimulating bacterial activity is usually considered as promoting soil health and fertility; however, microbes can also compete with roots for resources such as available N (Schimel and Bennett 2004) and oxygen (Naasz et al. 2008).

In our study, there was considerable variation in microbial N and SON data, which was due to their low levels compared with the very high concentration of NO₃⁻ in the soil. A mineral N concentration of 300–500 mg N kg⁻¹ is generally observed in growing media for greenhouse organic horticulture (Wang et al. 2017; Lévesque et al. 2018), but in our incubation jars, without any plant

Fig. 5. Time course of other biochemical parameters in a peat-based growing medium (A–G, O–T) and a mineral soil (H–N, U–Z) during the first 9 wk of the incubation. Dotted lines, at week 4, indicate the moment at which samples for metagenomic analysis were taken.

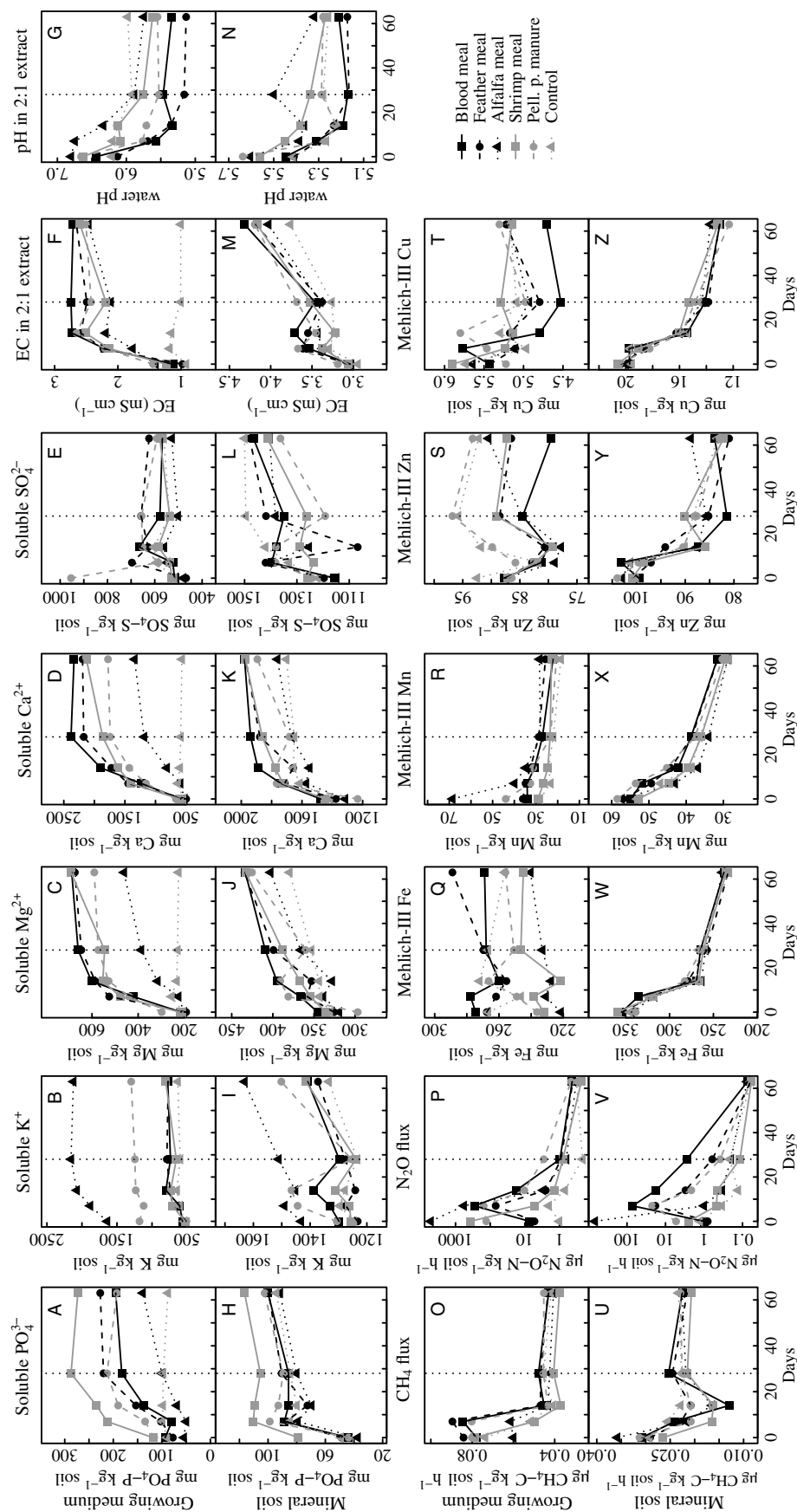
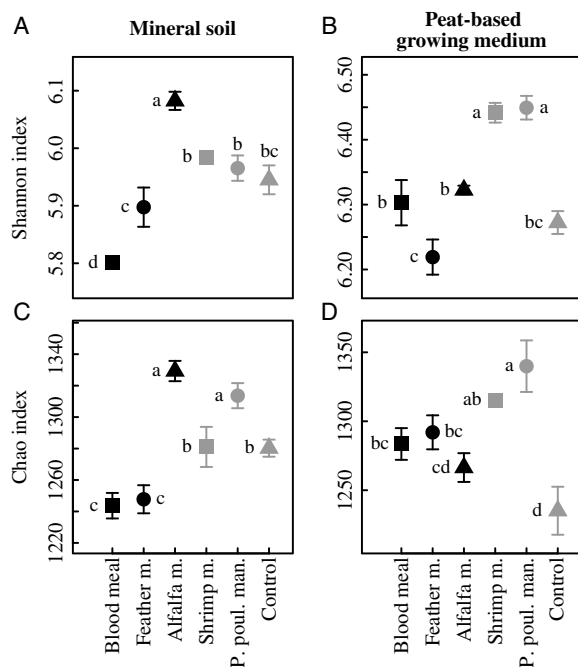


Fig. 6. Shannon (A and B) and Chao (C and D) diversity indexes for OTUs observed in the mineral soil (A and C) and peat-based growing medium (B and D). Sampling for metagenomic analysis was performed at week 4 of the incubation procedure. Data points with a same letter are not significantly different according to the least significant difference test ($\alpha = 0.05$). Values are mean indexes of four replicates per treatment (\pm standard deviation).



nutrient uptake, nitrate accumulated to concentrations greater than 1000 or 2000 mg N kg⁻¹ in the mineral soil and the organic growing medium, respectively. The discussion around microbial and SON is thus centered on corresponding C data, although interesting tendencies can still be observed on N data.

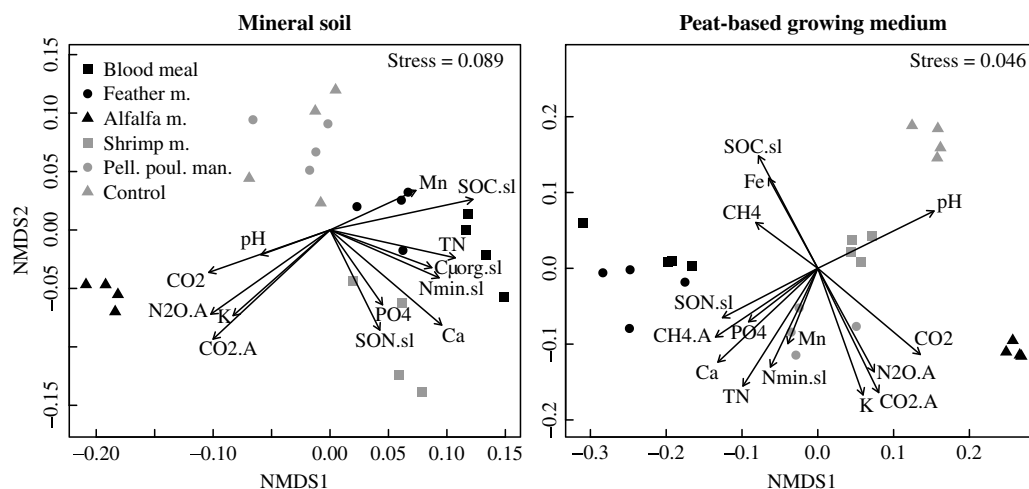
The N release following fertilizer application initially stimulated microbial activity (Zhang et al. 2017), as shown by the initial increase in CO₂ flux and the tendency of microbial biomass to increase after application of BM, FM, SM, and PM. However, as the microorganisms consumed the readily available C at a pace accelerated by N and C availability, C depletion eventually caused a drastic reduction in microbial biomass, hence the observed decrease in CO₂ flux (Figs. 2B and 3B). Söderström et al. (1983) and Ramirez et al. (2010) reported a similar phenomenon in laboratory experiments after urea applications. Moreover, in their studies, mineral sources of N caused an immediate decrease in soil respiration relative to the unfertilized control. Observing the same sharp changes in microbial biomass in situ is unlikely, as plants provide C themselves to the soil microorganisms (Badri and Vivanco 2009). In fact, a long-term increase in soil C in fertilized paddy soils was observed, even when only mineral N was applied (Tian et al. 2015). Nevertheless, organic

management increases the C content of soils on the long-term more than conventional management, both in greenhouse and field agriculture (Ge et al. 2011, 2013). Organic fertilizers thus have the potential to increase microbial biomass and activity, as long as organic matter is supplied periodically to the soil.

The effects of the five fertilizers on the soil bacterial community were generally more pronounced in the organic peat-based growing medium than in the mineral soil, because the applied fertilization per substrate mass was much higher, given its low bulk density compared with the mineral soil. Moreover, the residual N mineralization of previous fertilization inputs (before collecting the soil in the greenhouse) was lower in the growing medium than in the mineral soil. This reduced the background noise from residual mineralization of previously applied fertilizers in these cultivated soils. As organic fertilizers also bring nutrients other than N (Table 1), their use creates a range of nutritive conditions in the substrate, which influences the bacterial community (Kumar et al. 2018). Indeed, Grunert et al. (2016a) identified K and pH as two of the most important soil biochemical parameters controlling bacterial composition in conventional greenhouse growing media. Similarly, Bahram et al. (2018) reported that pH and mean annual precipitation are the most important determinants of soil microbial taxonomic composition on a global scale. Phosphate application can also induce a shift in microbial communities and modify their ecological functions (Ikoyi et al. 2018). In our study, K, pH, and phosphate indeed had a significant relationship with the composition of bacterial communities in both substrates, although the relationships were stronger in the peat-based growing medium. Calcium was the mineral element that had the strongest relationship with the bacterial communities in both substrates, closely followed by Mg in the peat-based growing medium and by K in the mineral soil. However, because Ca and Mg solubility is negatively linked to pH (Kunhikrishnan et al. 2016), it is expected to observe a higher concentration of soluble Ca and Mg in treatments that lead to a lower pH in the peat-based growing medium (e.g., BM and FM, see Figs. 5 and 7), unrelated to Ca and Mg concentrations in the fertilizer (Table 1).

In addition to our hypothesis that organic fertilizers with different chemical compositions would affect bacterial alpha diversity and the release of mineral N, the type of soil or growing medium appears to also influence the effect of the type of fertilizer on bacterial community. This suggests an interaction between the source of N and the type of substrate to which it is applied. In the mineral soil, where soluble C was less abundant (Table 2), AM supported the highest bacterial diversity and richness. In the organic growing medium, however, where soluble organic C was already abundant, SM and PM, containing a more balanced nutrient content (with P, Ca, or K), supported the highest bacterial diversity and richness. Differences in mineralization rates and microbial composition and activity are, of course,

Fig. 7. Nonmetric multidimensional scaling (NMDS) biplot of the bacteria OTU data, based on the Bray–Curtis dissimilarity matrix. Sampling for metagenomic analysis was performed at week 4 of the incubation procedure (four replicates per treatment). Biochemical variables presented are significantly linked to the composition of bacterial communities according to the Adonis test (permutational multivariate analysis of variance) and were fitted on the results of the NMDS ordination. Abbreviations (value at week 4 when not stated otherwise): Ca = soluble Ca^{2+} ; CH_4 = CH_4 flux at week 4; $\text{CH}_4.\text{A}$ = total CH_4 efflux from weeks 0 to 4; CO_2 = CO_2 flux at week 4; $\text{CO}_2.\text{A}$ = total CO_2 efflux from weeks 0 to 4; $\text{C}_{\text{org}}.\text{sl}$ = microbial C slope from weeks 0 to 4; Fe = Mehlich-III Fe; K = soluble K^+ ; Mn = Mehlich-III Mn; $\text{N}_2\text{O}.\text{A}$ = total N_2O efflux from weeks 0 to 4; $\text{N}_{\text{min}}.\text{sl}$ = mineral N slope from weeks 0 to 4; pH = pH in 2:1 water extract; PO_4 = soluble PO_4^{3-} ; $\text{SOC}.\text{sl}$ = soluble organic C slope from weeks 0 to 4; $\text{SON}.\text{sl}$ = soluble organic N slope from weeks 0 to 4; and TN = total soluble N.



expected in soils as different as a mineral soil and an organic growing medium. For conventional greenhouse growing systems, [Grunert et al. \(2016b\)](#) demonstrated that mineral and organic growing media supported different microbial communities. They further observed that different components of a growing medium support different functions of N mineralization (urea hydrolysis, nitrification), leading to varying N mineralization efficiency ([Grunert et al. 2016b](#)).

Conclusion

The mineralization rates presented in this paper provide new information for producers and agronomists for helping them to efficiently synchronize the availability of N in the soil or growing medium with crop N demand, especially in the context of organic greenhouse horticulture. In concordance with our hypothesis, the nutrient composition of organic fertilizers had an impact on the bacterial community which affected their N mineralization rate. We showed that AM, with its high C/N ratio, sustains microbial activity but provides a slow long-term N release and high greenhouse gas emissions. In contrast, BM and FM provide a fast and almost complete mineralization of their N, but without any increase of bacterial diversity. Shrimp meal and PM, with their P, K, and Ca contents, provide a better-balanced organic fertilization supporting diversified microbial communities and reducing the need for mineral inputs to sustain plant nutritional requirements other than N. Finally, all tested fertilizers support markedly divergent microbial

communities, probably as a result of the contrasting nutrient conditions that they provide. This variety of fertilizer properties encourages to rely on a combination of fertilizers in organic fertilization management. Further research should thus focus on the interaction and complementarity of the effects of those fertilizers on microbial composition and N availability.

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