BIOLOGICAL POTENTIAL AND DIFFUSION LIMITATION OF METHANE OXIDATION IN NO-TILL SOILS

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ABSTRACT

Prajaya Prajapati

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Long term no-till (NT) farming can improve the CH_4 oxidation capacity of agricultural lands through creation of a favorable soil environment for methanotrophs and diffusive gas transport. However, limited data is available to evaluate the merit of that contention. Although the potential for biological CH_4 oxidation may exist in NT soils, restricted diffusion could limit expression of that potential in fine-textured soils. A study was conducted to assess the CH_4 oxidation potential and gaseous diffusivity of soils under plow till (PT) and NT for > 50 years. Intact cores and composite soils samples (0-10 and 10-20 cm) were collected from NT and PT plots located at a well-drained site (Wooster silt loam) and at a poorly-drained (Crosby silt loam) site in Ohio. Adjacent deciduous forest soils were also sampled to determine maximum rate expected in undisturbed soils in the region. Regardless of study sites and soil depth, CH_4 oxidation rate (measured at near ambient CH_4) and oxidation potential (V_{max}, measured at elevated CH_4) were 3-4 and 1.5 times higher in NT than in PT soils, respectively. Activity in the NT soils approached (66-80 %) that in the forest soils. Half saturation constants (K_m) and threshold for CH_4 oxidation (Th) were lower in NT (K_m: 100.5 µL CH_4 L^{-1}; Th: 0.5 µL CH_4 L^{-1}) than in PT soils (K_m: 134 µL CH_4 L^{-1}; Th: 2.8 µL CH_4 L^{-1}) suggesting a greater affinity of long-term NT soils for CH_4, and a possible shift in methanotrophic community composition. CH_4 oxidation rates were lower in intact soil cores compared to sieved soils,

suggesting that CH_4 oxidation was limited by diffusion, a factor that could lead to lower field-measured CH_4 uptake than suggested by biological oxidation capacity measured in the laboratory. Regardless of soil drainage characteristic, long-term NT resulted in significantly higher (2-3 times) CH_4 diffusivity (mean: 2.5×10^{-3} cm^2 s^{-1}) than PT (1.5×10^{-3} cm^2 s^{-1}), probably due to improved soil aggregation and greater macro-pores volume in NT soils. Overall, these results confirm the positive impact of NT on the restoration of the biological (V_{max}, K_m and Th) and physical (diffusivity) soil attributes essential for CH_4 uptake in croplands. Long-term implementation of NT farming can therefore contribute to the mitigation of CH_4 emission from agriculture.

Pierre-Andre Jacinthe, Ph.D., Chair

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INTRODUCTION

Statement of the problem

Methane is a major greenhouse gas and an ozone-depleting substance. With a global warming potential (GWP) of 25 compared to CO_2 over a 100 year time horizon, CH_4 contributes an estimated 20% of the radiative forcing added to the atmosphere (IPCC, 2001; IPCC, 2007). Atmospheric CH_4 concentration has grown from 700 ppb at the beginning of industrial revolution in the 1850's to 1784 ppb in 2005 (IPCC, 2007). Both natural and anthropogenic sources contribute to atmospheric CH_4 increase (IPCC, 2001). Natural sources of CH_4 are mainly wetlands, while human-induced sources include rice paddies, enteric fermentation, natural gas exploration, landfills, sewage, and land management activities. Agricultural activities account for 50% of the global anthropogenic CH_4 emission (IPCC, 2001).

There are two significant sinks for atmospheric CH_4: the reaction with OH radicals in the troposphere estimated at 490±85 Tg y^{-1} (IPCC, 1996), and microbial oxidation in aerobic soils estimated at 40-60 Tg y^{-1} (Cicerone and Oremland, 1988; Schütz et al., 1990; IPCC, 2001). More recent assessments have estimated the biological CH_4 sink to be in the range of 30±15 Tg y^{-1} (IPCC, 1996; IPCC, 2001). Therefore, as a CH_4 sink, world soils contribution corresponds to just about 6-9 % of the total annual CH_4 removal from the atmosphere. However, despite the relatively small sink represented by CH_4 oxidation in soils, it is nearly the same magnitude as the net annual atmospheric CH_4 increase of 37 Tg y^{-1} (IPCC, 1996; IPCC, 2001).

In well aerated soils, CH_4 is oxidized by methanotrophs - a special group of soil bacteria that are unique in their ability to utilize CH_4 as a sole carbon and energy source.

Kinetic approach, phospholipid fatty acid (PLFA) profiles, DNA fingerprinting and C assimilation pathways (ribulose monophosphate pathway for type I and serine pathway in type II) have been used to categorize CH_4-oxidizers into type I and type II organisms (Hanson and Hanson 1996). Methanotrophs have also been categorized as high affinity microorganisms that can grow in low CH_4 environments, and low affinity methanotrophs that dominate in CH_4-rich systems such as landfills and rice fields (Bender and Conrad, 1992; Hanson and Hanson, 1996; Bull et al., 2000). Consumption of atmospheric CH_4 in upland soils has been found to be carried out by methanotrophs with K_m in the nanomolar (nM) range.

Methane can also be co-oxidized by autotrophic ammonia oxidizing bacteria (AAOB) with no apparent benefit to the cell (Bedard and Knowles, 1989; Hanson and Hanson, 1996). These AAOB microorganisms have a complete pathway for oxidation of ammonium (NH_4^+) to nitrite (NO_2^-) and derive their energy from that reaction. Apparent K_m values for CH_4 oxidation by AAOB are in the millimolar (mM) range (Bedard and Knowles, 1989; Hanson and Hanson, 1996), indicating much lower affinity for CH_4 compared to true methanotrophs

In agricultural and forest soils, CH_4 can be produced under anaerobic condition by methanogens either via CO_2 reduction or acetate fermentation (Conrad, 1996). Since both methanogenesis (production) and methanotrophy (consumption) can occur simultaneously, it is the difference in the intensity of these processes that determines the direction of CH_4 exchange between soil surface and the atmosphere. If production >> consumption, then soil is a net CH_4 source. Conversely, soil is a net sink (negative flux) when consumption exceeds production. Methane uptake in soils requires both favorable

soil biological and physical conditions. The biological component entails the presence of an abundant and active population of methanotrophs. The physical component refers to the development of soil physical conditions that are favorable for the transport of CH_4 and O_2 to methanotrophs.

Change in land use, especially the conversion of formerly undisturbed forest and grassland soils to farmland, has generally led to a decline in the CH_4 sink capacity of soils (Keller et al., 1990; Ojima et al., 1993; Singh et al., 2007). Various ecosystem studies have reported significantly higher CH_4 uptake rates in forest than in cultivated soils (Dobbie and Smith, 1996; Macdonald et al., 1996; Prime and Christensen, 1999). From CH_4 flux measurements at several study sites across Europe, Dobbie et al. (1996) reported a 60 % reduction in CH_4 oxidation when natural ecosystems were converted to agriculture. In the US Great Plains, Bronson and Mosier (1993) reported a 90 % reduction in CH_4 oxidation capacity of tilled soils under wheat (*Triticum aestivum*) and corn (*Zea mays*) compared to soils supporting native grassland. Oxidation of atmospheric CH_4 occurs in specific units (individual soil crumbs, sand grains covered by microbial bio-film) within the soil volume (Conrad, 1996). Frequent plowing leads to the destruction of these centers of methanotrophic activity when undisturbed natural ecosystems are converted to farmland. The extent of the decline in CH_4 oxidation due to cultivation also depends on the soil texture (Hutsch et al., 1996). Well aggregated and fine-textured soils generally offer greater protection to microorganisms and thus can better withstand disturbance, whereas sandy soils tend to easily lose methanotrophic activity when disturbed. In the light of these past studies (Bronson and Mosier, 1993; Dobbie et al., 1996; Hutsch et al., 1996) and considering the sensitivity of methanotrophs

to soil disturbance, it can be expected that reduced tillage could be beneficial for the restoration of methanotrophic activity in soils.

No-till (NT) farming represents a major shift in agricultural land management practices during last several decades. Unlike with conventional tillage farming or plow till (PT), annual plowing and seedbed preparation are eliminated under NT, and seeds are planted directly in the dead residue left by the previous crop. NT practice can bring remarkable changes in soil biological properties that can improve CH_4 oxidation. Commonly reported changes in soil biology with NT include soil organic carbon and nitrogen accretion, increased soil microbial biomass and greater enzyme activity (Dick et al., 1986; Feng et al., 2003). Along with all these improvements in soil properties, increased soil carbon availability and quality under NT can also stimulate the size and activity of the soil methanotrophic population (Conrad, 1984; Hutsch et al., 1993).

No-till adoption also brings numerous improvements in soil physical properties, including greater stability of soil structure, larger soil aggregates, and greater soil macro-porosity (Mahboubi and Lal, 1998). The lack of tillage disturbance under NT is conducive to the formation and preservation of water-stable soil aggregates (Fengyun et al., 2011). West et al. (1992) reported 50 % to 67 % higher water stable aggregates in soils under NT compared to conventional tillage. Similarly, Mahboubi and Lal (1996) found water stable soil aggregate to be consistently higher (regardless of season) under NT compared to moldboard plow (PT). Similar trends were reported by others (Bruce, 1990; Unger, 1994) - that is, higher stability of soil aggregates under NT compared to conventional tillage (PT). Therefore, given the positive impact of NT on soil aggregation and the relationship between aggregation and porosity (Lal et al., 1994; Ball et al.,

1997b), more efficient soil-atmosphere exchange of gases can be expected in soils under NT. Thus, from the above discussion, one can expect that both the biological and physical soil attributes required for CH_4 uptake to be present at a higher level in NT soils compared to soils under conventional tillage.

No-till farming has been viewed as a practice that has the potential to off-set GHGs emission (CH_4 in particular) from the agricultural sector without decreasing land productivity (Cole et al., 1997; Council of Agricultural Science and Technology, 2004). Conservation tillage practices such as no-till (NT) and chisel till (CT) are increasingly being adopted due to their profitability and environmental benefits over PT (CTIC, 2012). No-till farming has grown in popularity during the past three decades with 35 % of the US farmland under NT in 2009 (USDA, 2010). However, limited information is available regarding the effects of NT on GHG emission (Johnson et al., 2005; Venterea et al., 2005).

A number of studies have shown that fertilizers containing ammonium (NH_4^+) can lead to a reduction in soil CH_4 oxidation (Bronson and Mosier 1994; Hutsch et al. 1994). However, other experiments have shown no effect (Lessard et al., 1997; Stiehl-braun et al., 2011), transient effects (Hartmann et al., 2010) or even a positive effect of N application (Bodelier et al, 2000), indicating that the effect of N fertilization on CH_4 oxidation in soils is complex and may be confounded with other soil properties (Bodelier and Laanbroek, 2004). Although the underlying mechanisms of these effects remain unclear, it has been speculated that in the short term, NH_4^+ may interfere with the CH_4 monooxygenase enzyme (MMO), but repeated N application may, in the long run, induce

a shift in soil methanotrophic composition resulting in low CH_4 oxidation (Adamsen and King, 1993).

CH_4 flux measurements in upland soils have generally shown considerable seasonal variability (Prieme and Christensen, 1997). Seasonal fluctuation in CH_4 flux has generally been attributed to change in soil moisture and temperature - physical factors that control CH_4 production and transport. Soil moisture influences CH_4 uptake by controlling the diffusion of atmospheric CH_4 and O_2 in the soil profile (King and Adamsen, 1992; Adamsen and King, 1993). Soil moisture limits CH_4 and O_2 diffusion by occupying the small pore networks and then the macro-pores at high soil moisture. Due to the slow rate of gaseous diffusion in water and the low water solubility of CH_4, elevated soil moisture can effectively block CH_4 movement in soils. On the other hand, extreme water deficit can reduce soil CH_4 uptake due to the physiological stress imposed by dry soil conditions on soil microbes (Nesbit and Breitenbeck, 1992). Soil temperature is an additional factor explaining the seasonal fluctuation in CH_4 uptake reported in several studies (Castro et al. 1995; Prieme and Christensen 1997). However, the influence of temperature on CH_4 oxidation tends to be much stronger in high CH_4 environments (landfills, bogs, Born et al., 1990; Crill et al., 1994) than in upland soils exposed to near ambient atmospheric concentration (Steudler et al., 1989; Sitaula et al., 1995).

Gas movement in soil is controlled by convective and diffusive processes. Convective processes can dominate during transient periods of atmospheric pressure change, and at locations where subsurface geologic or biologic gas sources are substantially large (Hillen, 1998). Diffusion - the movement of gaseous molecules due to concentration gradient - is the dominant process controlling the movement of gases

through the soil profile, and the exchange of gases between soil and the atmosphere. Gas diffusivity is a property that expresses the rate of gas movement through soils and, in the context of this study, the transport of O_2 and CH_4 to the sites of CH_4 oxidation within the soil volume (Dorr et al., 1993; Kruse et al., 1996).

Diffusion controls the supply of CH_4 to the microorganisms responsible for its oxidation (Ball et al., 1997a; Ridge-well et al., 1999). For a given soil type, gas diffusivity and air-filled porosity are related to bulk density, soil moisture content soil structure, and the connectivity of soil pores (Ball and Smith 1991; Czepiel et al., 1995). Past studies have shown that, more than total porosity, the large soil pores (macro-pores) are the main contributor to gaseous transport in soils. Jacinthe and Lal (2006) reported a negative relationship between soil macro-pore volume and CH_4 fluxes in a meadow, underscoring the improvement in soil CH_4 uptake with greater availability of large soil pores. Borken and Brumme (1997) reported a significant increase in CH_4 oxidation due to amelioration in soil structure following lime application to forest soils.

Under NT, the decomposition of crop residue left on the soil surface is generally slow due to limited mixing with other soil constituents and decomposers (Gregorich et al., 2006). Thus, accumulated residue and litter may act as a diffusion barrier to gaseous exchange in NT systems (Ball et al., 1999). This, in addition to reports of increased soil bulk density and thus lower total soil porosity under NT (Cassel, 1982; Tebrugge and During, 1999; Wander and Bollero, 1999), would suggest that gaseous exchange may be impeded in NT soils. Further, as a source of labile organic substrate, the presence of surface residue could stimulate soil biological activity, leading to the development of O_2-deficient pockets in NT soils where CH_4 production can take place. These physical

factors could therefore result in lower CH_4 uptake under NT in comparison to PT, despite the improvement in soil biology that NT farming could bring.

Once a soil is disturbed, the loss of CH_4 oxidation capacity persists for long periods ranging from months (Willison et al., 1995), years (Mosier et al., 1991; Hutsch et al., 1994; Chan and Parkin, 2000; Regina and Alakhu, 2010) or decades (Ojima et al., 1993; Kruse and Iversen, 1995; Omonode et al., 2007). Most studies have shown that the restoration of CH_4 oxidation capacity of previously cultivated soils is a slow process requiring several decades (Prieme et al., 1997; Hutsch, 1998). The slow recovery may be due to the difficulty to remediate the damage sustained by methanotrophs (Sitaula et al., 2000), and to the slow development of favorable soil structure following disturbance (Mapa, 1995). Damages to methanotrophic community include the destruction of ecological niches most suitable to methanotrophs, and possible shifts in the soil microbial population due to a progressive replacement of methanotrophs by nitrifiers, especially in cultivated soils subjected to annual N fertilizer application (Castro et al., 1994).

Due to the absence of soil physical disturbance, it has been suggested that the CH_4 sink capacity of cultivated soils can be restored with NT adoption. Although available results are mixed, this assumption is nevertheless supported by the studies of Mosier et al. (2006) and Ussiri et al. (2009) in which soils under NT acted as significantly stronger CH_4 sink compared to similar soils under conventional tillage. A more recent evaluation at several sites across Ohio has shown a progressive increase in CH_4 uptake with NT duration (Shrestha et al., 2013). Data from that study (Shrestha et al., 2013, unpublished) have also shown that the mean CH_4 uptake at 2 experimental plots under NT for 48 years was 7 times lower at location with poorly drained soil (-0.021 mg CH_4-C m^{-2} d^{-1}) than at

location with well-drained soil. These results suggest a possible diffusion limitation of CH_4 uptake at the poorly drained location. Therefore, even though soils under NT may have the potential for biological CH_4 oxidation, this potential may be masked by diffusion restriction.

So far, the mechanisms by which tillage practice affect soil CH_4 uptake are not completely understood. Restoration of CH_4 uptake with NT farming may be due to positive changes in soil microbial properties (microbial biomass, species composition, cell-specific activity of methanotrophs) and/or improvement in soil diffusivity due to increased soil macro-porosity. This study was conducted to develop a better understanding of the improvement in both soil biology and soil diffusivity with the adoption of NT farming.

Project significance

NT farming has been viewed as a promising option to mitigate GHG emission in the agricultural sector. But, consideration of long-term NT as a strategy to minimizing the adverse effects of cultivation on soil CH_4 sink strength is still a working hypothesis. The benefits of NT farming on several soil quality parameters are well documented, but there is a paucity of data regarding the impact of NT on GHG fluxes, and more specifically on the soil factors controlling CH_4 oxidation in NT soils. Many studies (Kessavalou et al., 1998; Mosier et al., 2006; Jacinthe and Lal, 2008; Ussiri et al., 2009) have reported recovery of CH_4 uptake capacity after adoption of NT. Yet, less is known whether the restoration is mediated by improvement of soil biology or better gas transport properties. This study will improve our understanding of the mechanisms controlling CH_4 uptake in

NT soils, and will help reduce the uncertainties regarding the overall impact of NT agriculture on regional GHG budget.

Very few studies have been carried out to assess the impact of tillage on the CH_4 uptake capacity of soils under long-term NT independently of other management practices. The proposed study provides a unique opportunity to assess the CH_4 oxidation potential of soils under long-term NT in comparison to soils under conventional tillage practices (PT). Soil samples for this study were from research plots that have been under NT for about 50 years - to our knowledge, this is the longest running continuous NT experiment in the world. Experimental plots are under different tillage methods but all other management practices (crop, fertilizer) are similar. No previous evaluation of the impact of tillage on CH_4 oxidization capacity has been made using soils under NT for such a long period of time. Results of the proposed study will be a valuable contribution to society and agricultural sciences.

Research questions and hypotheses

1. How does long term adoption of NT affect the methane oxidation capacity of soils?

With the absence of soil disturbance for a long period of time, it is hypothesized that a large and active population of methanotrophs will evolve, resulting in increased CH_4 oxidation.

2. How does tillage practice and soil type affect diffusion of CH_4 in soils?

Methane uptake in upland soils depends upon optimum transport of CH_4 and O_2 to methanotrophs. The transport of these gases is expected to vary with soil type. It is therefore hypothesized that, due to improved soil aggregation, gas diffusivity will be

significantly greater in NT compared to PT soils. However, due to increase in bulk density and higher moisture content, NT can lead to lower soil diffusivity in fine-textured and poorly-drained soils.

Research objectives

The specific objectives of this research study are as follows:

1. To characterize the methane oxidation potential of NT soils in comparison to PT.
2. To assess the significance of diffusion restriction on CH_4 oxidation in NT soils.

MATERIAL AND METHODS

Site Description

This study was carried out with soil samples collected in 2012 from experimental plots located near the towns of South Charleston (39°45', 83°36'W) and Wooster (40°45'48"N, 81°54'20"W) in Ohio (USA). These plots were established by the Ohio Agricultural Research and Development Center (OARDC) to study the effect of tillage practices on land productivity and soil properties. Tillage practices investigated include no-till (NT), chisel till, and conventional moldboard plow (PT). Tillage treatments were distributed in a randomized complete block design with four replicate plots per treatment (Van Doren et al., 1976; Dick, 1983). Experimental plots measure 8.4 x 37 m at the Wooster site, and 5 x 61 m at South Charleston. The experimental plots have been under continuous corn (*Zea mays L.*) since their establishment in 1962. The climate at each site is continental (Ohio Agronomy Guide, 1988). Long-term (30 y) mean annual temperature and precipitation are 10.7 °C and 1,104 mm at South Charleston, and 10.2 °C and 1,020 mm at Wooster, respectively. At the Wooster site, soil is predominantly well-drained silty loam classified as Wooster (Fine, mixed, mesic Aeric Epiaqualfs) and Canfield (Fine-loam, mixed, mesic Aquic Fragiudalfs). At the South Charleston site, however, soil is poorly-drained and classified as Crosby (Fine-loamy, mixed, mesic Oxyaquic Fragiudalfs). Soil texture information at the study sites is reported in Table 1. General characteristics of soils at the locations are reported in Mahboubi et al. (1993).

Since the experimental plots have been under the same tillage practice for the same length of time but have contrasting soil drainage characteristics (moderately well drained in Wooster and somewhat poorly drained in South Charleston), they offer a

unique opportunity to evaluate the effect of soil drainage on CH_4 oxidation and associated soil properties.

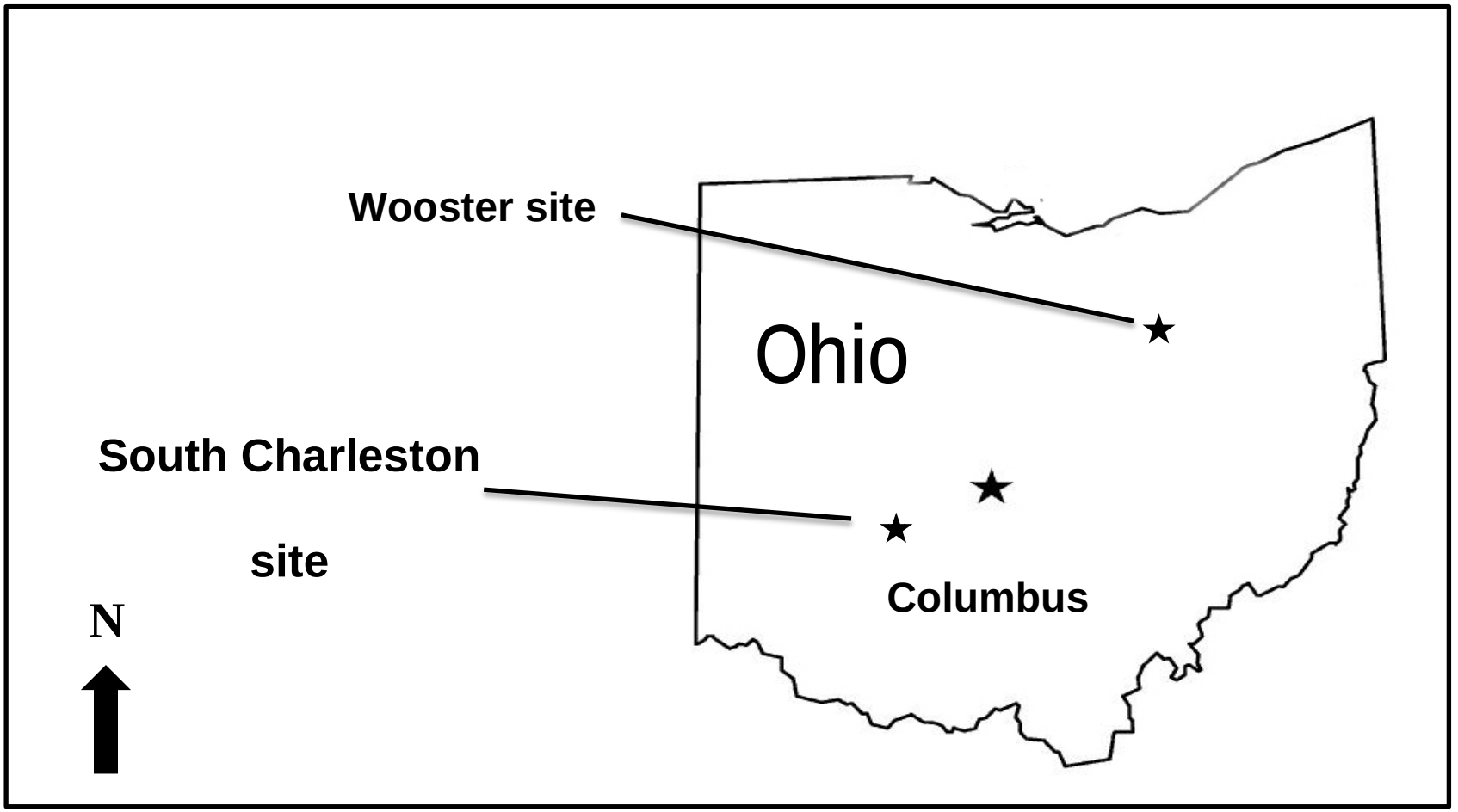
Table 1. Surface soil texture at the study sites

Parameter	South Charleston	Wooster
Soil classification	Crosby silt loam (Aeric Ochraqualf)	Wooster silt loam (Typic Fragiudalf)
Slope	1%	2.5 - 4.5 %
Sand (%)[a]	15	25
Silt (%)	65	60
Clay (%)	20	15

[a] Mineral soil composition data are from Mahboubi et al. (1993)

In the present study, two tillage practices were investigated: no-till (NT), and conventional tillage (or plow till, PT). Soil samples were also collected from a secondary growth deciduous forest (hereafter referred to as woodlot, WL) located near the experimental plots. The woodlots are treated as reference sites during data analysis and interpretation to represent the maximum oxidation potential of undisturbed soils in the region.

Fig 1. Location of the study sites in Ohio.



Soil sampling

Soil samples were collected on two occasions: summer and fall 2012. Soil samples (composite and intact soil cores) were collected from the 0-10 cm and 10-20 cm soil depths. For each tillage practice, three plots were selected for the collection of soil samples and, within each plot, samples were extracted from 2 sampling points. For each depth, soil material from these six sampling points was thoroughly mixed to make one composite soil sample per tillage practice. At the woodlot, soil samples were also collected at six randomly selected sampling points. Next to each sampling point, an intact core (5 cm diam., 5 cm length) was also extracted for determination of bulk density. This sampling procedure was adopted in order to capture natural site variability. The summer sampling occurred on June 6 (Wooster) and June 13, 2012 (South Charleston). Sieved soil samples were used for assessing CH_4 oxidation kinetics and soil intact cores for determining soil gas diffusivity. In addition, sieved soil samples were also used for determination of background soil properties at the study sites.

A second soil sampling was conducted during the fall of 2012 (Wooster on November 23 and South Charleston on November 29). Composite soil samples were collected using the sampling procedure described above and was used to assess seasonal variation in CH_4 oxidation capacity. For each tillage treatment, 6 intact soil cores (3 from surface and 3 from subsurface) were also collected for assessment of CH_4 oxidation capacity and possible limitation of diffusion on the process. A similar number of intact cores were also obtained for the woodlots. Cores were covered with parafilm to reduce evaporative water loss, and

composite soil samples were stored in plastic bags. All samples were transported in a cooler over ice pads, and stored in a laboratory refrigerator at 4 ^{o}C until used.

Physicochemical properties of soil

Bulk density was determined by the core method. Intact soil cores were placed in an oven (105 ^{o}C), and allowed to dry for at least 72 h. Bulk density was computed as the ratio of the dry weight of soil to core volume. Soil pH was measured with a pH meter (Accumet 25, Fisher Scientific) using a soil suspension (2:1 water to soil ratio). Gravimetric soil moisture content was determined by oven drying 5 g moist sample in aluminum trays (105 ^{o}C, 48 h). Gravimetric moisture (θ) was computed as:

$$\left(\frac{W_1 - W_2}{W_2}\right)$$

where, W_1= weight of moist soil, W_2 = weight of dry soil. Total porosity (Ø) was computed by equation:

$$\left(1 - \frac{\rho_b}{2.65}\right)$$

where, ρ_b is bulk density. Air-filled porosity (ε_a, cm^3 cm^{-3}) was determined by deducting gravimetric moisture content from total soil porosity:

$\varepsilon_a = \emptyset - \theta$.

Total carbon (TOC) and total N (TN) were measured by dry combustion (900 ^{o}C) using a Vario-TOC Cube analyzer (Elementar Inc., NJ). Oven-dried soil samples were sieved to a fine powder (150 µm), and approximately 8-12 mg of soil material was used for analysis. Soil material was transferred into tin capsules

and pressed into pellets. The exact weight of the pellets were measured with a micro-balance (Mettler Toledo) and recorded. Then the pellets were loaded into the carousel in Vario-TOC Cube analyzer. Each sample was analyzed in duplicate.

Microbial biomass carbon (MBC) was determined using the substrate-induced respiration (SIR) procedure (Anderson and Domsch, 1978). Duplicate field moist soil (20 g) was placed in a beaker and amended with 600 mg of glucose-talc (1:4) mixture. The beaker content was thoroughly mixed with a glass rod, and placed inside a mason jar (volume: 900 mL). After 30 minutes of acclimation, each jar was closed with a lid fitted with a sampling port and was incubated at room temperature (25 ^{o}C). After 2 h, air samples from each jar headspace were taken and stored in evacuated gas vials. Air samples were analyzed for CO_2 concentration using gas chromatography. MBC was computed as:

$$\text{SIR} = \left(\frac{\mu\text{L CO}_2}{\text{Lh}}\right)\left(\frac{0.45\,\text{L}}{\text{dwg soil}}\right)$$

Where, dwg = dry weight of soil, g; MBC, mg biomass-C kg^{-1} soil = 40.04 SIR (Anderson and Domsch, 1978)

Mineral Nitrogen

The pool of mineral N (NO_3^- and NH_4^+) in soil sample was determined using the KCL extraction procedure. Field-moist soil (10 g) was weighted in a disposable centrifuge tube and mixed with 40 ml of 1M KCl. The suspension was shaken for 1 h at 200 rpm on a shaker. The suspension was allowed to settle, and

then was filtered using Whatman no.1 filter placed in a glass funnel. The extracts were collected in scintillation polypropylene vials. All the extracts were stored frozen until analyzed. Nitrate content was determined using a Konelab (Aquakem 250) analyzer.

Ammonium concentration was measured spectro-photometrically using the micro-plate procedure described by Sims et al. (1995). Quadruplicate 100 µL aliquots of each sample were transferred to a 96 well micro-plate. Each well then received 25 µL of a citrate reagent (5 g citric acid and 2 g NaOH in 100 ml of water). After waiting for 1 min, 50 µL of nitroprusside reagent (7.183 g of sodium salicylate and 0.125 g Na nitroprusside in 100 mL water, pH adjusted to 6-7 with NaOH) was added to each well. After standing for 20 min, 25 µL of hypochlorite (1g Na_3PO_4 dissolved in 2 mL of 2 M NaOH, 10 mL of bleach and water to bring to 100 mL, pH adjusted to 12-13 with NaOH). After standing for 40 min for color development, the absorbance was read on a spectrophotometer (Versamax, Sunnyvale, CA) at a wavelength (λ) of 650 nm. A standard curve was developed using solutions of known NH_4^+ concentration against absorbance. Using this standard curve, respective NH_4^+ concentration in soil extracts were calculated based on absorbance reading.

Determination of methane oxidation potential

Methane oxidation potential was assessed using intact soil cores and field-moist sieved (5 mm) samples. Field-moist sieved (20 g of 2-5 mm size soil aggregates) soil samples were placed in 900 mL wide-mouth Mason jars. For each

soil sample, incubation was conducted at five different initial CH_4 concentrations (range: 3 to 300 µL CH_4 L^{-1}) in the jar headspace. Various amounts of methane (from a main stock of 990,000 µL CH_4 L^{-1} and subsequent stock made from the main stock) were added to obtain the targeted starting concentration in the jar headspace. Three jar replicates were used for each initial targeted CH_4 oxidation. Change in CH_4 concentration was monitored over a period of 7-8 days. Air samples were taken using gastight syringes (15 mL), and stored in crimp-sealed evacuated glass vials (10 mL) fitted with butyl rubber septa. Air samples were analyzed for CH_4 and CO_2 by gas chromatography (Varian CP 3800). In general, decrease of methane concentration in all the soil samples followed a first-order decay model

$$A = A_o e^{-kt}$$

Where, "A" is concentration of substrate (CH_4) at time "t", "A_o" is the initial CH_4 concentration (at t = 0) and k is the rate constant (k, h^{-1}). Rate constant was computed using non-linear regression procedure (NLIN available in SAS, 2012). Rate of CH_4 oxidation (µL CH_4 L^{-1} h^{-1}) was computed as a product of rate of constant (k) and corresponding initial CH_4 concentration.

Using the same non-linear regression procedure (NLIN procedure, SAS 2012), rate of CH_4 oxidation (v) and initial CH_4 concentration (S) were fitted to the Michaelis-Menten model to derive maximum oxidation rate (V_{max}) and half saturation constant (K_m):

$$v = \left(\frac{V_{max} S}{K_m + S} \right)$$

To determine kinetic parameters, attempts were made to fit the data to the Lineweaver and Burk plot (linear form of the Michaelis Menten model). The procedure was found non satisfactory for a large number of samples. Therefore, as proposed by Ranaldi et al., (1995; 1999), nonlinear regression methods were used to derive kinetic parameters. Saturation curves [that is rate (v) vs. substrate [S]) were drawn using the Sigma plot (2009) graphing and statistical software (Systat Software Inc, San Jose, CA).

Sieved soil samples from the 10-20 cm layer were allowed to incubate for close to 400 h to determine the CH_4 oxidation threshold (Th) defined as the CH4 concentration below which no CH_4 oxidation occurs. The threshold value (Th) for CH_4 oxidation was obtained through examination of the CH_4 decay curve for the soil samples incubated at near ambient CH_4 concentration (3 µL CH_4 L^{-1}) and for close to 400 h. "Th" value was determined by inspecting the CH_4 consumption curve down to the lowest CH_4 value at which CH_4 concentration in the incubation vessel remained constant for more than 2 days.

Methane oxidation was also investigated using intact soil cores, but with one initial CH_4 concentration (3-4 µL CH_4 L^{-1}). Methane concentration during the incubation period was fitted to a first order model and oxidation rate was computed as described above. Results of the CH_4 oxidation assays conducted with sieved soil were compared to those obtained with intact cores in order to assess the impact of diffusion limitation on CH_4 consumption.

When sieved soil was incubated at an initial CH_4 concentration of 3 µL CH_4 L^{-1} during the CH_4 oxidation assays, the rate of CO_2 production was taken as

a measure of basal soil respiration. Air samples (20 mL) were taken periodically (7-8 times over an 8-9 day period) from jar head space and analyzed for CO_2 by gas chromatography. CO_2 concentration (μL CH_4 L^{-1}) obtained was plotted against time (h) to determine the slope of the regression line (ppm CO_2 h^{-1}). Basal soil respiration (BSR) was expressed as mg CO_2-C kg^{-1} soil h^{-1} taking into account the incubation jar volume and gravimetric soil moisture content.

Determination of soil gas diffusivity

For this assessment, intact soil cores collected in November 2012 were used, and CH_4 was the diffusing gas. Since the soil cores contain both CH_4-producing and CH_4-consuming microorganisms, sterilization was necessary to overcome calculation errors that might be caused by biological activity. Therefore, soil cores were taken to a gamma radiation facility at Purdue University in West Lafayette (IN) for sterilization. The soil cores were loaded inside a radiation chamber which delivered 2 Megarads (20 kGy) of radiation over a period of approximately 80 hours. Soil cores were sterilized by direct and indirect action. In direct action, the ionizing event causes direct damage to cell DNA inducing a mutagenic or lethal effect. Indirect effects can occur as a result of radiolysis of cellular water and the formation of active oxygen species, free radicals and peroxides causing single double strand DNA breaks (Jackson et al., 1967; Romanovskaya et al., 1999). Sterilized cores were carried back to the Soil Biogeochemistry laboratory in Indianapolis with caution and stored in a refrigerator.

Gaseous diffusivity of soils was determined using the procedure proposed by Rolston et al. (1978). A diffusion apparatus was assembled, and included an intact soil core securely fastened between two boards made of PVC material. A plastic gasket was placed around the lip of the aluminum cylinder containing the soil core to ensure air-tight contact between soil core and the PVC boards. Each soil core was interfaced with 2 jars: one representing the CH_4 source and the other the sink (Fig. 1). For the source jar, CH_4 was added (40 ml of 99 % CH_4) to bring CH_4 concentration to 24×10^3 µL CH_4 L^{-1} at the beginning of a run. To prevent convective flow of the gas, a volume of 40 mL of ambient air was added to the sink jar. Because of the concentration gradient created, this set-up allowed a constant flow of CH_4 from the source to the sink jar through the intact soil core. Each diffusion run lasted 7-9 days to complete.

Air samples (15 ml) were taken from the headspace of the sink and the source jars and transferred to evacuated glass vials for CH_4 analysis. The data were fitted to a first order diffusion model:

$$\ln (C_{source} - C_{sink}) = kt$$

where, C_{source} is the concentration of sink at time t; C_{sink} is the concentration of source at time t = 0 ; k = first order rate constant (min^{-1}); t = time (min). The rate constant "k" was calculated by using slope function in the Excel 2010

($\ln (C_{source} - C_{sink})$ vs. time)

The diffusion coefficient (D_s, cm^2 s^{-1}) was determined using the model proposed by Rolston et al. (1978) for diffusion of gases through porous media:

$$K = D_s \frac{A}{VL}$$

where, A is the cross sectional area of soil core (cm^2); V is the volume of diffusion chamber (liter), L is the thickness of soil sample (cm).

Analytical methods

Air samples were analyzed for CO_2 and CH_4 using a Varian (CP-3000) gas chromatograph interfaced with a Combipal headspace auto-sampler. The stationary phase consisted of a Hayesep DB column (300 cm long, 0.3 cm id) connected to a thermal conductivity detector (100 ^oC, for CO_2 detection) in series with a flame ionization detector (FID at 150 ^oC, for CH_4 detection). Analytical conditions were: carrier gas (Helium: 20 mL min^{-1}), flame gases (Hydrogen: 25 mL min^{-1} and hydrocarbon-free compressed air: 300 mL min^{-1}) and oven temperature 90 ^oC.

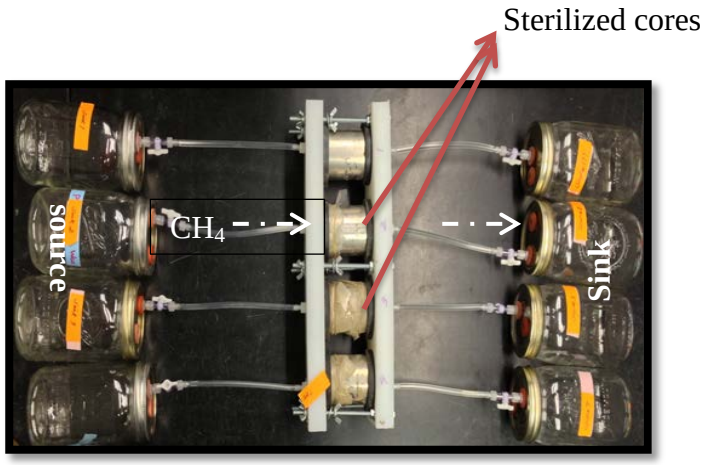


Fig 2. Experimental set up for estimation of soil gas diffusivity in soil cores

Statistical Analysis

Data was analyzed using two-way ANOVA PROC GLM procedure available in SAS (SAS Institute, 2012) with tillage and study site as experimental

factors at two depths: 0-10 cm and 10-20 cm. In the analysis, response variable were SOC, TN, bulk density, NH_4-N, NO_3^-, moisture, V_{max}, K_m, CH_4 oxidation rate and BSR. Sample sets not large enough for ANOVA were compared using paired t-test. Statistical significance was determined at $P < 0.05$.

RESULTS

General properties of soil

Soils used in the study were slightly acidic to neutral (pH: 5.7-7.4, Table 2 and 3). The bulk density (ρ) of soils ranged from 1 to 1.5 g cm^{-3}. Significant effect of tillage on bulk density was detected. Bulk density was significantly higher in PT plots than in NT plots (Table 2 and 3).

In the surface soil layer (0-10 cm), SOC was significantly higher in NT than in PT soils. The opposite was observed in the 10-20 cm layer (Table 2 and 3). There was no significant effect of tillage in TN. In most of the cases, C/N ratio was generally higher in woodlot soils and lowest in PT soils (Table 2 and 3).

Mineral nitrogen at the study sites

NH_4-N was higher in the woodlots (both the surface and the subsurface layers) at the South Charleston site whereas, no particular trend was seen in the Wooster plots. A significant effect of the tillage and its interaction with site were observed with regard to nitrate (NO_3^-) concentration.

Soil moisture content

Soil moisture content varied significantly with sites and tillage practices both in the June and November sampling events (Table 5). Regardless of the sites and sampling dates, moisture content followed the order WL > NT > PT. Moisture content was generally higher in the samples collected in November than

in June (Table 5). Soils from the South Charleston site had consistently higher soil moisture compared to soils from Wooster.

Soil respiration (BSR) and microbial biomass carbon (MBC) in relation to tillage, soil type and season

Significant effects of tillage on biochemical soil properties (for MBC and BSR, $P < 0.001$) were detected. The effects varied with site and the soil properties considered (Table 7). Regardless the of sites and depths, soil respiraiton was 2 fold greater in NT than in PT in the surface layer. MBC decreased with increasing intensity of tillage disturbance and followed the order: WL > NT > PT (Fig. 2).

The rate of CO_2 production in soil samples incubated at near ambient CH_4 was taken as a measure of soil respiration. Results from incubation of the soil samples collected in June, 2012 were used to examine the effect of tillage and soil type on soil respiration. In addition, results obtained in June were compared with that of November to examine the effect of season on soil respiration. While no significant effect of location on MBC was found, the location of sites had significant effect on soil respiration. In general, soil repiration was greater in soil from the moderately well-drained Wooster site compared to the poorly drained soil from South Charleston.

Methane oxidation as related to soil biochemical properties

Interrelationships between CH_4 oxidation (rate and V_{max}) and physical soil properties (NH_4-N, NO_3^-, SOC, BSR, MBC, TN, C/N and D_s) were examined using linear regression analysis. At both sites, CH_4-oxidation was strongly related ($r^2 > 0.6$, $P < 0.05$) to MBC, BSR and D_s (Table 9). With the South Charleston soils, CH_4 oxidation capacity and V_{max} were positively related to NH_4-N. However, negative relationship between inorganic nitrogen and CH_4 oxidation was observed at the Wooster site.

Table 2. Physico-chemical properties of soils at the South Charleston experimental plots.

Tillage	Soil property [a]				
	pH	SOC [b] (g C kg^{-1} soil)	TN (g C kg^{-1} Soil)	C/N	Bulk density (g cm^{-3})
0-10 cm					
WL	7.4 (0.5)	31.4 (0.0)**a**	2.3 (0.1)	13.7	1.0 (0.1)**b**
NT	6.7 (0.4)	23.4 (0.1)**b**	2.1 (0.1)	11.1	1.1 (0.1)**b**
PT	6.4 (1.1)	11.8 (0.0)**c**	1.5 (0.0)	7.9	1.4 (0.2)**a**
10-20 cm					
WL	6.1 (0.2)	9.7 (0.2)**c**	1.2 (0.0)	8.1	1.1 (0.0)**b**
NT	5.8 (0.3)	10 (0.0)**b**	1.3 (0.0)	7.7	1.2 (0.2)**b**
PT	7.4 (0.3)	12.3 (0.3)**a**	1.7 (0.0)	7.2	1.5 (0.1)**a**

[a] pH Values are mean of 2 measurements. All other values are mean of 3 measurements with standard deviation in parenthesis.
[b] In a given column and soil depth, values followed by different letters are significantly different at $P < 0.05$.

Table 3. Physico-chemical properties of soils at the Wooster experimental plots.

Tillage	Soil property [a]				
	pH	SOC [b] (g C kg^{-1} soil)	TN (g C kg^{-1} Soil)	C/N	Bulk density (g cm^{-3})
0-10 cm					
WL	5.7 (0.2)	25.6 (0.8)**a**	2.1 (0.3)	12.2	1 (0.1)**b**
NT	6.4 (0.1)	21.4 (0.0)**b**	2.1 (0.0)	10.2	1.1 (0.2)**b**
PT	6.9 (0.1)	13.6 (0.2)**c**	1.8 (0.0)	7.6	1.3 (0.3)**a**
10-20 cm					
WL	6.5 (0.1)	13.3 (0.2)**c**	1.8 (0.0)	7.4	1.1 (0.4)**b**
NT	6.9 (0.0)	13.9 (0.3)**b**	1.7 (0.3)	8.2	1.2 (0.1)**b**
PT	7.3 (0.1)	16.7 (0.0)**a**	1.7 (0.1)	9.8	1.4 (0.3)**a**

[a] pH Values are mean of 2 measurements. All other values are mean of 3 measurements with standard deviation in parenthesis.
[b] In a given column and soil depth, values followed by different letters are significantly different at $P < 0.05$.

Table 4. Mineral nitrogen content in soils at the South Charleston and the Wooster plots at the time of soil sampling in June 2012.

Tillage	Soil property [a]			
	South Charleston		Wooster	
	NH_4-N [b] (mg NH_4-N kg^{-1} Soil)	NO_3^- (mg NO_3^- kg^{-1} Soil)	NH_4-N (mg NH_4-N kg^{-1} Soil)	NO_3^- (mg NO_3^- kg^{-1} Soil)
0-10 cm				
WL	7.3 (0)	11.7 (0.4)**c**	9.0 (0)	25.2 (0.7)**b**
NT	6.2 (3)	16 (3.0)**b**	7.6 (4.5)	14.7 (0.4)**c**
PT	4.7 (1.5)	25.4 (9.7)**a**	11.8 (3.2)	34 (1.3)**a**
10-20 cm				
WL	8.9 (4.9)	17.8 (0.6)**a**	7.2 (0.2)	5.2 (0.4)**c**
NT	3.7 (1.3)	23.0 (0.4)**a**	8.3 (2.4)	21.6 (3.5)**b**
PT	4.6 (0.7)	19.7 (0.6)**a**	7.8 (1)	29.9 (1.6)**a**

[a] Values are means of 3 measurements with standard deviation in parentheses.
[b] In a given column and soil depth, values followed by different letters are significantly different at $P < 0.05$.

Table 5. Temporal variation in soil moisture at the study sites.

Tillage	Moisture [b]			
	South Charleston		Wooster	
	June [b]	Nov	June	Nov
0-10 cm				
WL	29.5 (1.0)**a**	33.1 (1.3)**a**	23.1 (0.2)**a***	31.5 (2.1)**a***
NT	24.5 (1.3)**b**	25.6 (1.9)**b**	19.8 (1.4)**b**	21.2 (0.2)**b**
PT	14.6 (1.0)**c***	19.5 (0.7)**c***	14 (0.7)**c**	17.6 (0.8) **b**
10-20 cm				
WL	24.5 (1.1)**b**	25.8 (0.4)**a**	21.1 (1.4)**a**	24.3 (0.4)**a**
NT	22.6 (1.3)**a**	24.9 (0.1)**b**	18.8 (1.7)**a**	20.1 (0.2)**b**
PT	19.7 (0.8)**ab**	20.9 (0.2)**c**	15.8 (1.5)**a**	18.5 (2.1)**b**

[a] Values are means of 3 measurements with standard deviation in parenthesis.
[b] In a given column and soil depth, values followed by different letters are significantly different at $P < 0.05$.
* Pair that are significantly different at $P < 0.05$

Table 6. Two-way ANOVA results for soil physico-chemical properties.

Class Variables	df	Response Variables						
		SOC	TN	Bulk density	NH_4-N	NO_3^-	Moisture (%)	
							June	Nov
Depth (0-10)								
Site	1	***	NS	NS	NS	***	***	*
Tillage	2	***	NS	***	NS	***	***	***
Site X Tillage	2	**	NS	NS	NS	***	*	NS
Depth (10-20)								
Site	1	***	*	NS	NS	***	**	**
Tillage	2	***	NS	***	NS	***	*	***
Site X Tillage	2	***	NS	NS	NS	***	NS	NS

*P < 0.05, **P < 0.01, ***P < 0.001, NS = Not significant

Table 7. Two way ANOVA results for soil biological and physical properties.

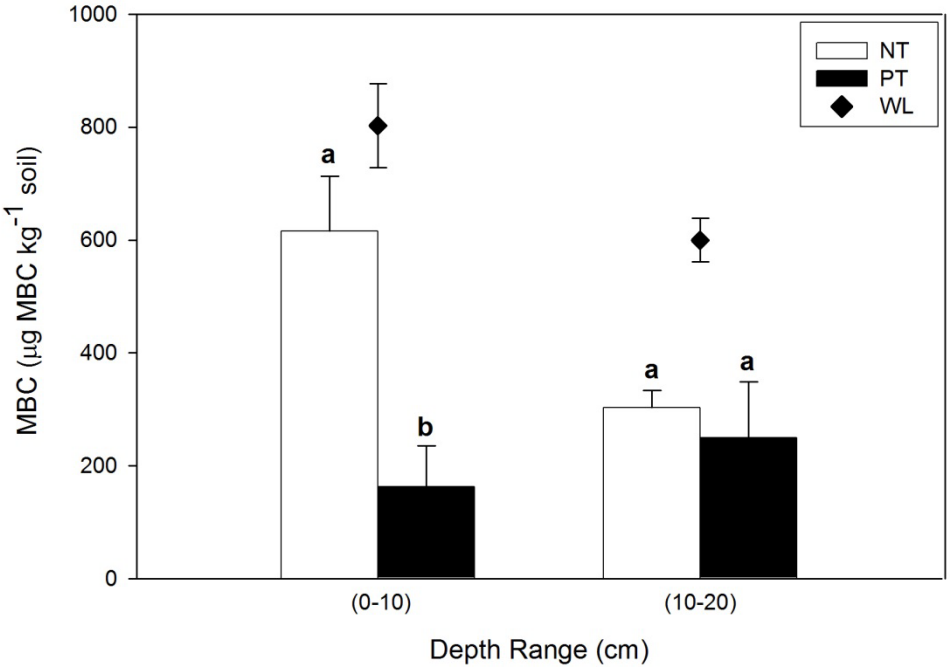
		Response Variables					
Class Variables	**df**	**MBC**	**V_{max}**	**K_m**	**$(CH_4)_R$[a]**	**BSR**	**D_S**
Depth (0-10)							
Site	1	NS	***	NS	***	***	NS
Tillage	2	***	***	***	***	***	***
Site X Tillage	2	NS	NS	NS	***	***	NS
Depth (10-20)							
Site	1	NS	***	NS	***	***	NS
Tillage	2	***	***	***	***	***	***
Site X Tillage	2	NS	*	NS	***	*	NS

*P < 0.05, **P < 0.01, ***P < 0.001, NS = Not significant

[a] rate of methane oxidation in sieved soils

Fig 3. Microbial biomass carbon (MBC) at the South Charleston and Wooster sites as related to tillage practice. For a given soil depth, vertical bars with different letters are significantly different.

a. South Charleston



b. Wooster

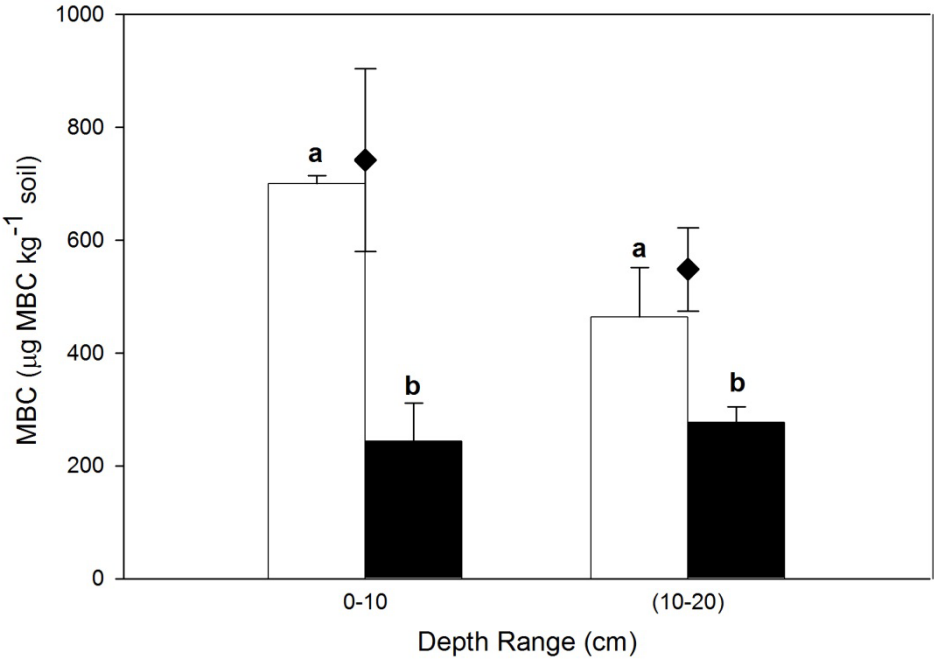


Table 8. Basal soil respiration (CO_2-C kg^{-1} soil hr^{-1}) at the study sites as related to land-use and tillage practice. Each value is mean of 2 replicates.

Land-use	Tillage	Location			
		South Charleston		Wooster	
		June [a]	Nov	June	Nov
0-10 cm					
Woodlot	WL	0.93**a***	0.88**a**	1.18**a**	0.96**a**
Cropland	NT	0.34**b**	0.33**b**	0.36**b**	0.35**b**
Cropland	PT	0.16 **c**	0.15**c**	0.24**c**	0.19**c**
10-20					
Woodlot	WL	0.35**a**	0.33**a**	0.47**b**	0.47**a**
Cropland	NT	0.27**b**	0.25**b**	0.53**a**	0.32**b**
Cropland	PT	0.19**c**	0.17**c**	0.22**c**	0.17**c**

[a] Within a column and for each soil depth, values followed by different letters are significantly different at $P < 0.05$.

[*] BSR in soil samples collected in June and November at both the sites was not significantly different for all the observation when tested with paired t-test at $P < 0.05$.

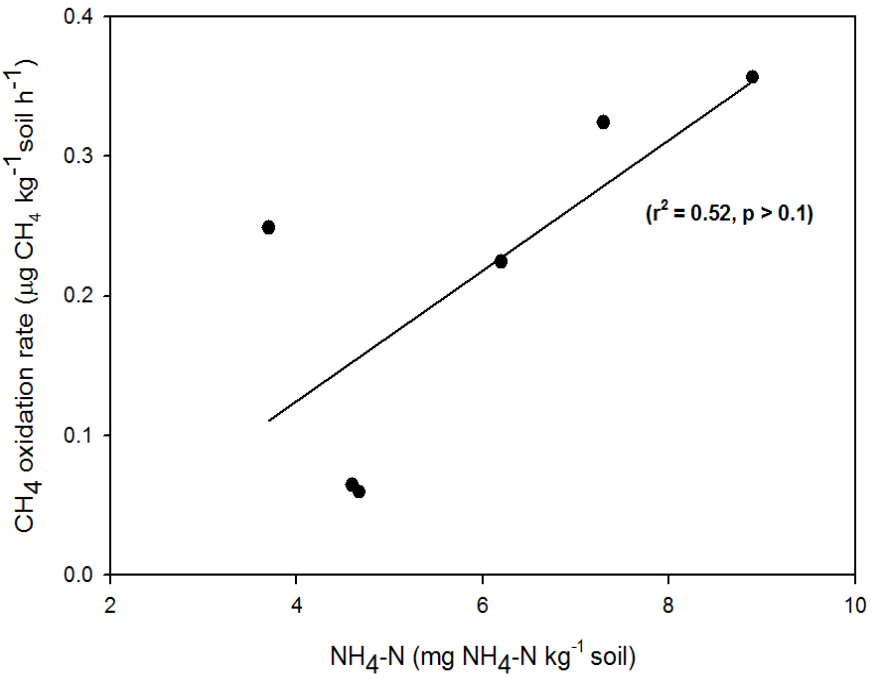
Table 9. Coeffient of determination (r^2) for the relationships between CH_4 consumption and soil properties.

Site	Variables	SOC	TN	C/N	NH_4-N	NO_3^-	MBC	BSR	$CH_{4(R)}$ [b]	D_s
South Charleston										
	$CH_{4(R)}$	0.1	0.003	0.24	**0.53**	(-) 0.15	**(0.67)**	**(0.83)**	1	**(0.66)**
	V_{max} [c]	0.005	(-) 0.02 [d]	0.05	0.17	(-) 0.13	0.17	0.14	**(0.81)**	0.47
Wooster										
	$CH_{4(R)}$	0.08	0.18	0.03	(-) 0.31	(-) 0.64	**(0.7)**	**(0.75)**	1	**(0.68)**
	V_{max}	0.014	0.06	0.0002	(-) 0.30	(-) 0.6	0.24	0.28	**(0.95)**	0.65

[a] Regression coefficients greater than **0.50** are in bold letters and those that are significant at **5 %** are listed in parentheses.
[b] Rate of methane oxidation
[c] Maxiumum rate of methane oxidation
[d] (-) Negative relationship

Fig 4. Relationship between CH_4 oxidation rate and NH_4-N at a) South Charleston, and b) Wooster.

a. South Charleston



b. Wooster

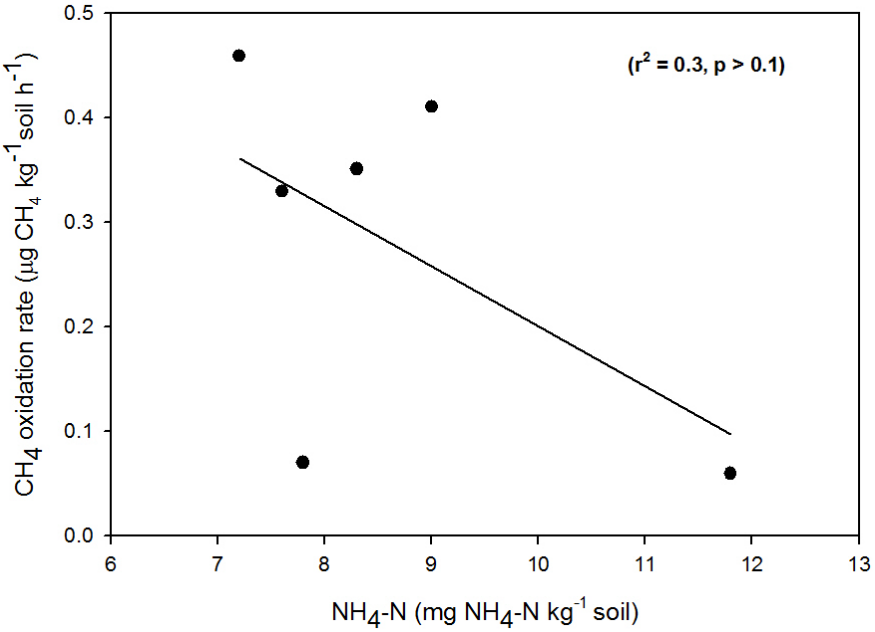
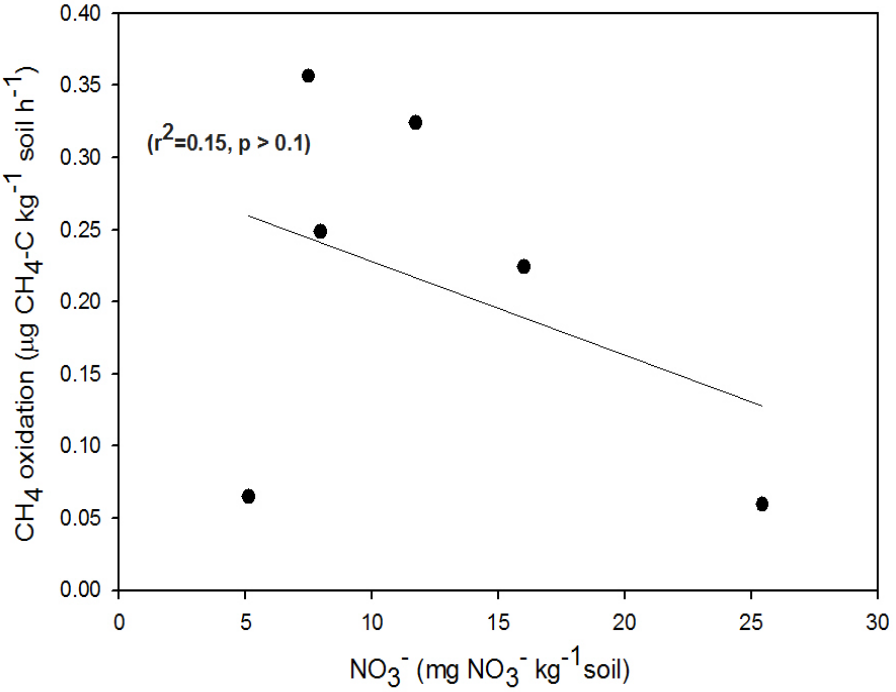
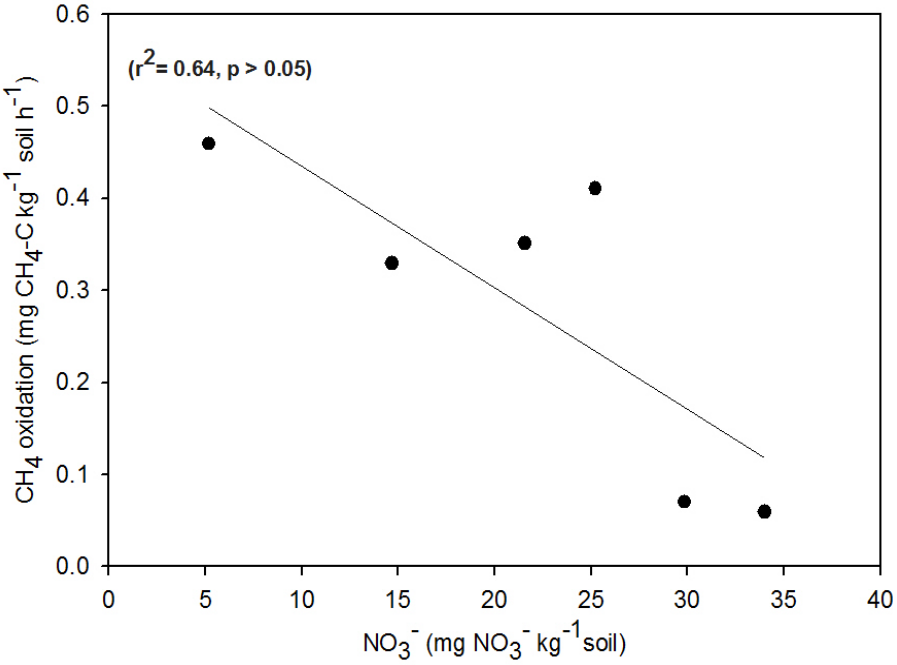


Fig 5. Relationship between CH_4 oxidation rate and NO_3-N at a) South Charleston, and b) Wooster.

a. South Charleston



b. Wooster



Soil CH_4 diffusivity

Tillage practices had a significant effect ($P < 0.01$) on soil-CH_4 diffusivity. Irrespective of the study sites, diffusivity was significantly greater in NT soils compared to PT soils (Fig. 5). Overall, soil-CH_4 diffusivity was 2-3 fold greater in NT compared to PT soils. Diffusivity was higher in soils from the moderately well-drained Wooster plots compared to the poorly-drained South Charleston plots, but difference was not statistically significant.

Air-filled porosity (ε_a) differed significantly between tillage practice. Despite higher soil moisture, air-filled porosity was significantly higher in NT than in PT soils (Fig. 6). In some cases, air-filled porosity values in NT soils were even greater than in WL soils, indicating larger pore volume in NT soils. Regression analysis showed a strong linear ($r^2 = 0.8$, $P < 0.001$) relationship between soil-gas (CH_4) diffusivity and air-filled porosity.

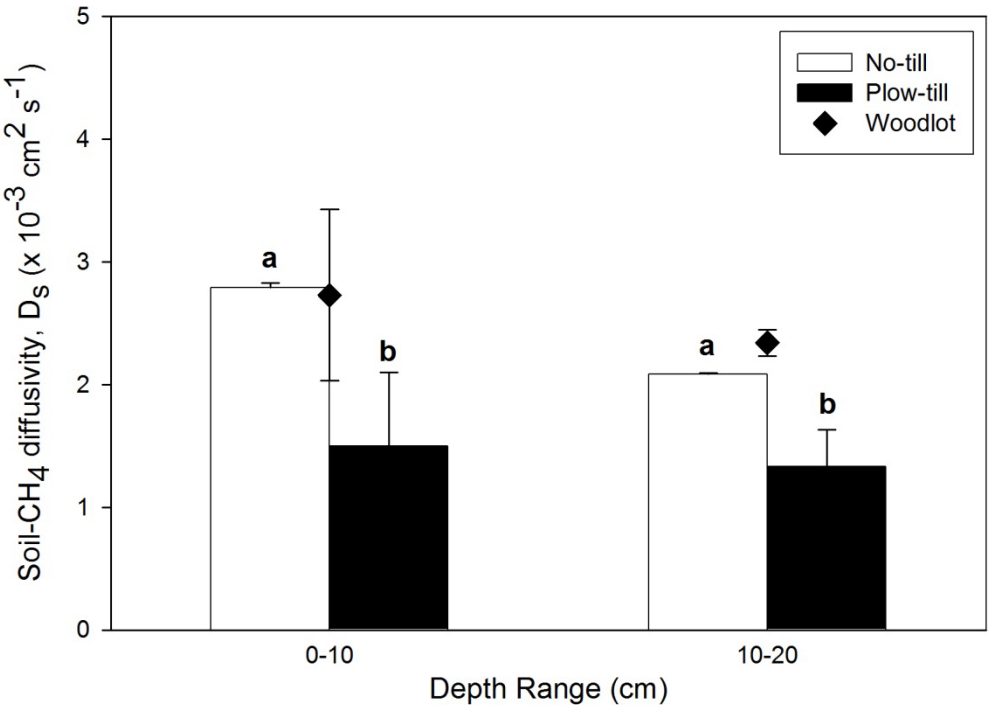
Methane oxidation kinetics

All the soil samples tested, irrespective of the tillage practices and land-use, manifested some ability to oxidize methane. In general, CH_4 consumption followed a first order kinetic model. Variation in CH_4 concentration in jar headspace typically followed a concave pattern (Fig. 8). In the case of WL and NT soils, the concavity was more pronounced when incubation was conducted with a high (~ 250 μL CH_4 L^{-1}) initial methane concentration (Fig. 8). Consumption of CH_4 by PT soils also followed a first order model but, due to very low rates [rate constant (k) in the order of 10^{-4} h^{-1}], the decay curve was seemingly linear when incubation was conducted at near ambient CH_4

concentration. However, at higher initial CH_4 concentration (~ 250 µL CH_4 L^{-1}), some degree of concavity was observed even with the PT soils suggesting greater methanotrophic activity with increased availability of CH_4.

Fig 6. Soil-CH_4 diffusivity in intact cores from the (a) South Charleston and (b) Wooster sites as related to tillage. Vertical bar with different letter indicates values that are significantly different.

a. South Charleston



b. Wooster

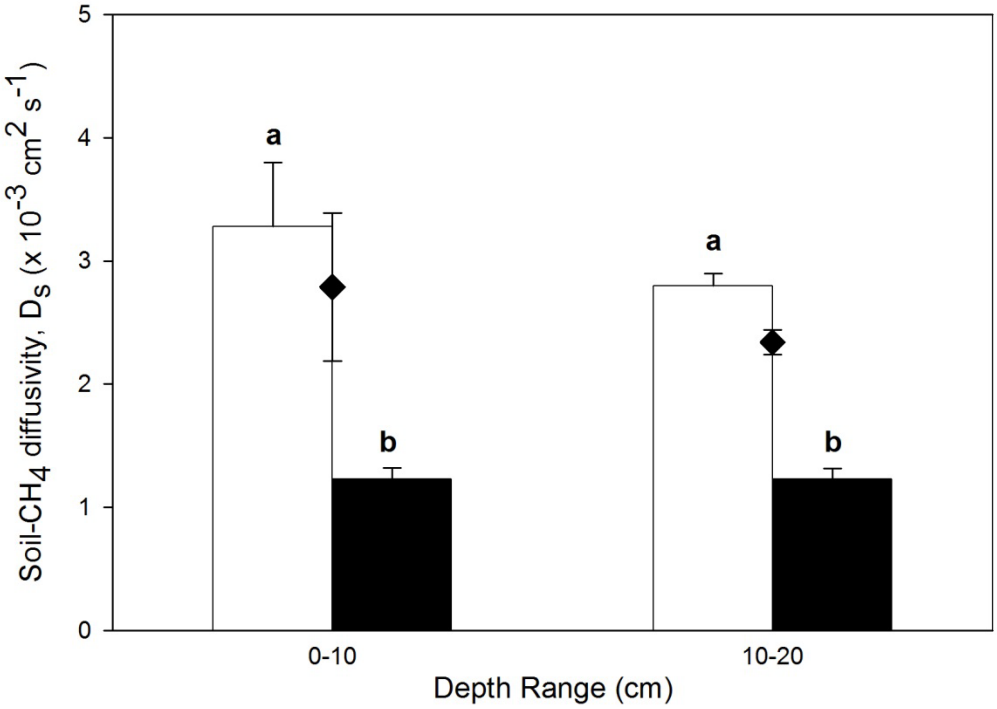


Fig 7. Relationship between soil-CH_4 diffusivity (measured with intact cores) and air-filled porosity. The regression line is drawn using data for all types of land-use and tillage practices.

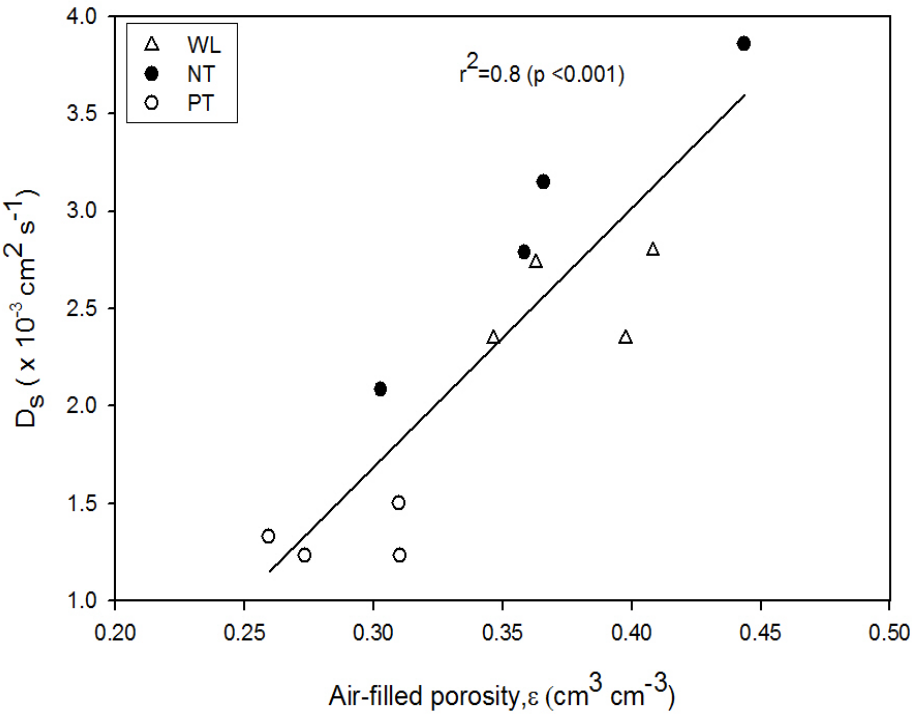


Fig 8. Time line of CH_4 consumption at initial concentration of 3 µL CH_4 L^{-1}. Panel a = 0-10 cm depth; panel b = 10-20 cm depth. Th_w, Th_n, and Th_p are the threshold values for Woodlot, NT and PT soil samples, respectively.

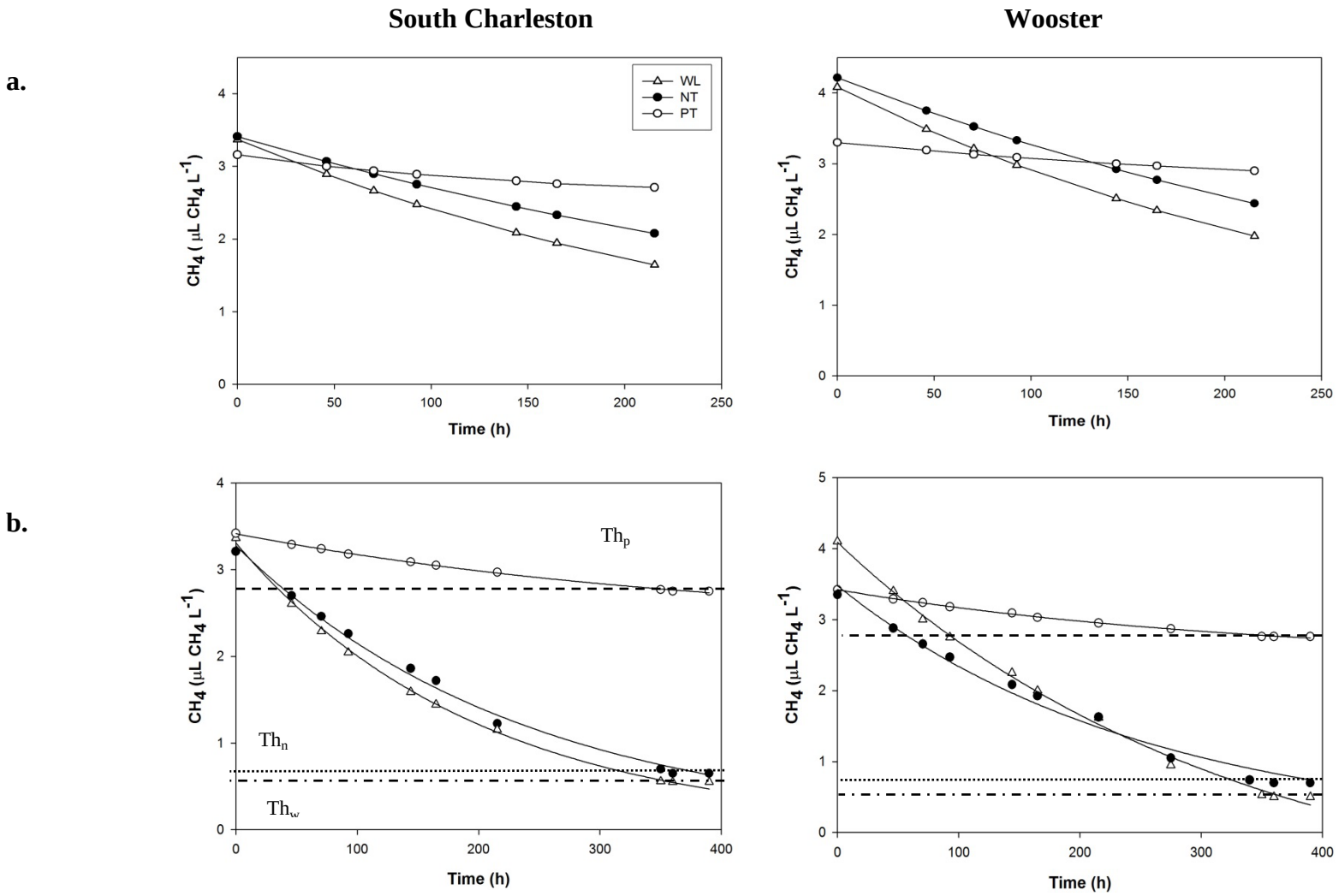
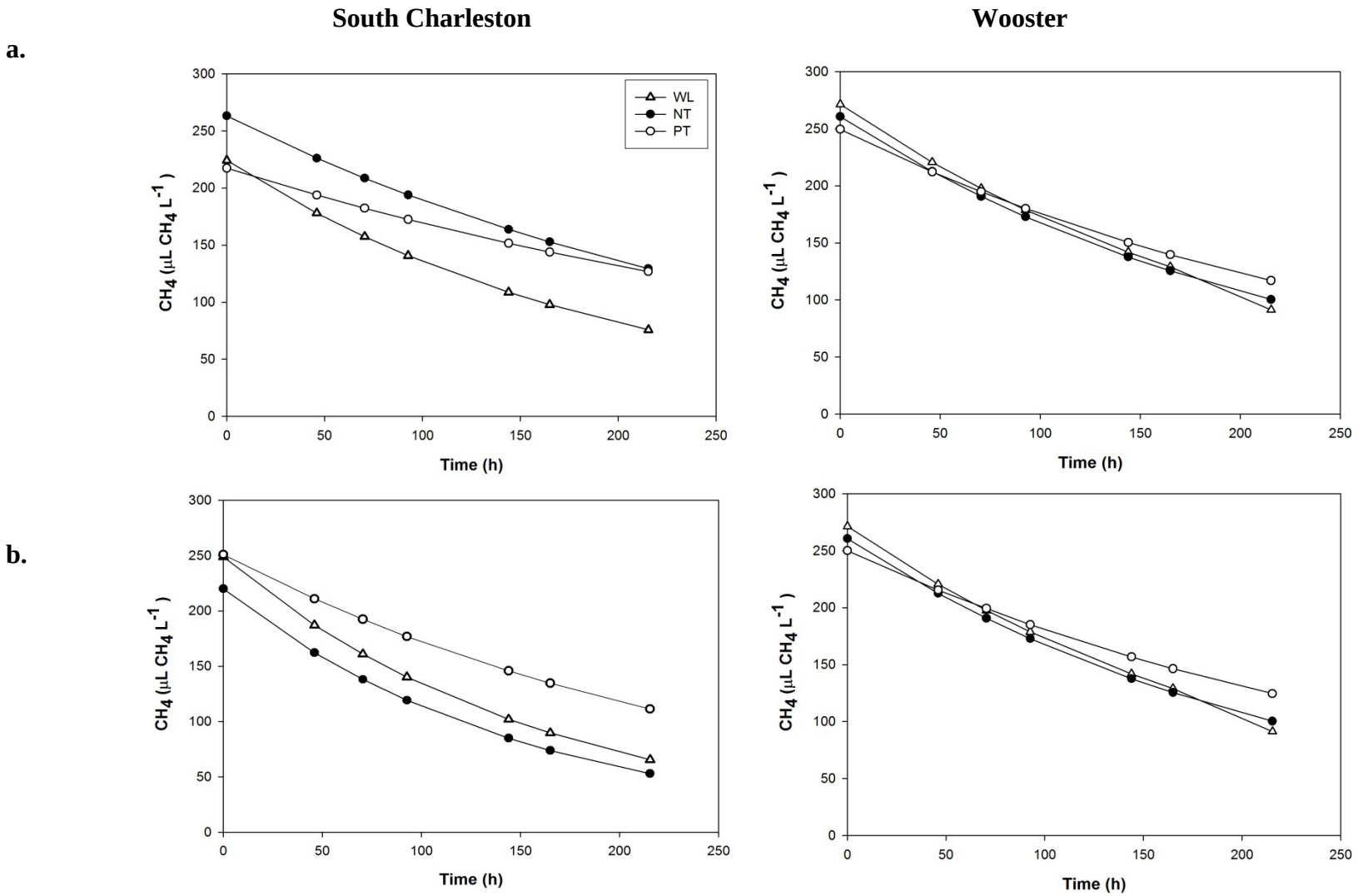


Fig 9. Time line of CH_4 consumption at intial concentration of 250 µL CH_4 L^{-1}. Panel a = 0-10 cm depth; panel b = 10-20 cm depth.



Kinetic parameters of CH_4 oxidation as related to tillage and soil type

Maximum rate of methane oxidation (V_{max}) differed significantly ($P < 0.001$) with regard to tillage practices and land use (Table 10). Across study sites, V_{max} was (1.5 times) greater in NT than in PT soils. Further, a significant effect of study sites on V_{max} was detected (Fig. 10 and Table 10), with the well-drained Wooster soil exhibiting higher V_{max} than the poorly-drained Crosby soil (South Charleston).

Values obtained for the half saturation constant (K_m) differed significantly between the two tillage practices. K_m values were consistently lower in NT than in PT soils. Overall, the K_m ranking was in the order: WL < NT < PT. This ranking suggests higher MMO enzyme activity and greater affinity of methanotrophs for CH_4 in soils with less physical disturbance.

Measured thresholds (Th) for CH_4 oxidation were significantly lower in NT than PT soils (Fig. 8b). Overall, the threshold values for NT soils (0.6 µL CH_4 L^{-1}) were ~ 4 fold lower than for PT soils (2.7 µL CH_4 L^{-1}) but were similar to the Th values recorded with forest soils (0.5 µL CH_4 L^{-1}).

Methane oxidation rate of soils as affected by tillage and soil type

The effect of tillage and soil type on the CH_4 oxidation capacity of soils was examined using results obtained at low (3-4 µL CH_4 L^{-1}) initial CH_4 concentration. Oxidation rates (µg CH_4-C kg^{-1} h^{-1}) were significantly ($p < 0.001$) higher in NT soils than in PT soils (Table 3). Mean oxidation rates were 3-4 fold greater in NT than in PT soils. Under NT, the sub-surface soil layers showed higher oxidation rate than the surface layers. In plots under PT, CH_4 oxidation was uniformly distributed throughout both soil

layers. Irrespective of landuse and tillage practices, the moderately-well drained Wooster soil exhibited higher CH_4 consumption capacity than the poorly-drained Crosby soil found at the South Charleston site (Fig. 11).

Temporal variation in methane oxidation capacity of soils

Incubation of the soil samples collected in June and November were carried out at near ambient CH_4 level (3-4 µL CH_4 L^{-1}) to examine temporal variation in CH_4 oxidation. In general, rates of CH_4 oxidation were generally higher in soils collected in June than in November (Table 13) but ANOVA showed no significant effect of sampling date. However, regardless of sampling date and study site, the effect of tillage practices on CH_4 oxidation persisted (higher rate in forest and NT soils than in PT soils).

Diffusion limitation in intact core compared to sieved soil

Diffusion limitation was assessed by comparing CH_4 oxidation rates in intact cores with those measured in sieved soils. In all cases, rates of CH_4 oxidation were significantly (3-4 fold) lower in the intact cores compared to sieved soils suggesting diffusion restriction of CH_4 transport in the intact cores (Fig. 12).

Regardless of sites and soil depths, CH_4 oxidation rate in intact cores extracted from WL and NT plots was 34-44% of that in sieved soils. However, with intact cores from the PT plots, oxidation rate in intact cores was between 20 % (Wooster) and 6 % (South Charleston) of the rate measured with sieved soils. These results illustrate the severe restriction of gaseous diffusion on CH_4 oxidation in PT soils, especially at poorly-drained locations.

Interrelationships between methane oxidation, bulk density and soil-gas diffusivity

Regression analysis showed a strong positive relationship ($r^2 = 0.68$, $P < 0.001$) between CH_4 oxidation in cores and soil-CH_4 diffusivity (Fig. 14). In comparison to PT cores, NT and WL cores showed higher diffusivity values and corresponding higher CH_4 oxidation rates. In contrast, negative relationships were observed between bulk density and diffusivity ($r^2 = 0.6$, $P < 0.001$, Fig. 13a), and between bulk density and CH_4 oxidation ($r^2 = 0.7$, $P < 0.001$, Fig. 13b). These results are consistent with the other indications of gas transport restriction stated above.

Fig 10. Maximum rate of CH_4 oxidation (V_{max}) in soils from the South Charleston (left) and Wooster (right) sites. Panel a = suface 0-10 cm; Panel b = subsuface 10-20 cm. Vertical bar represents standard deviation of the mean.

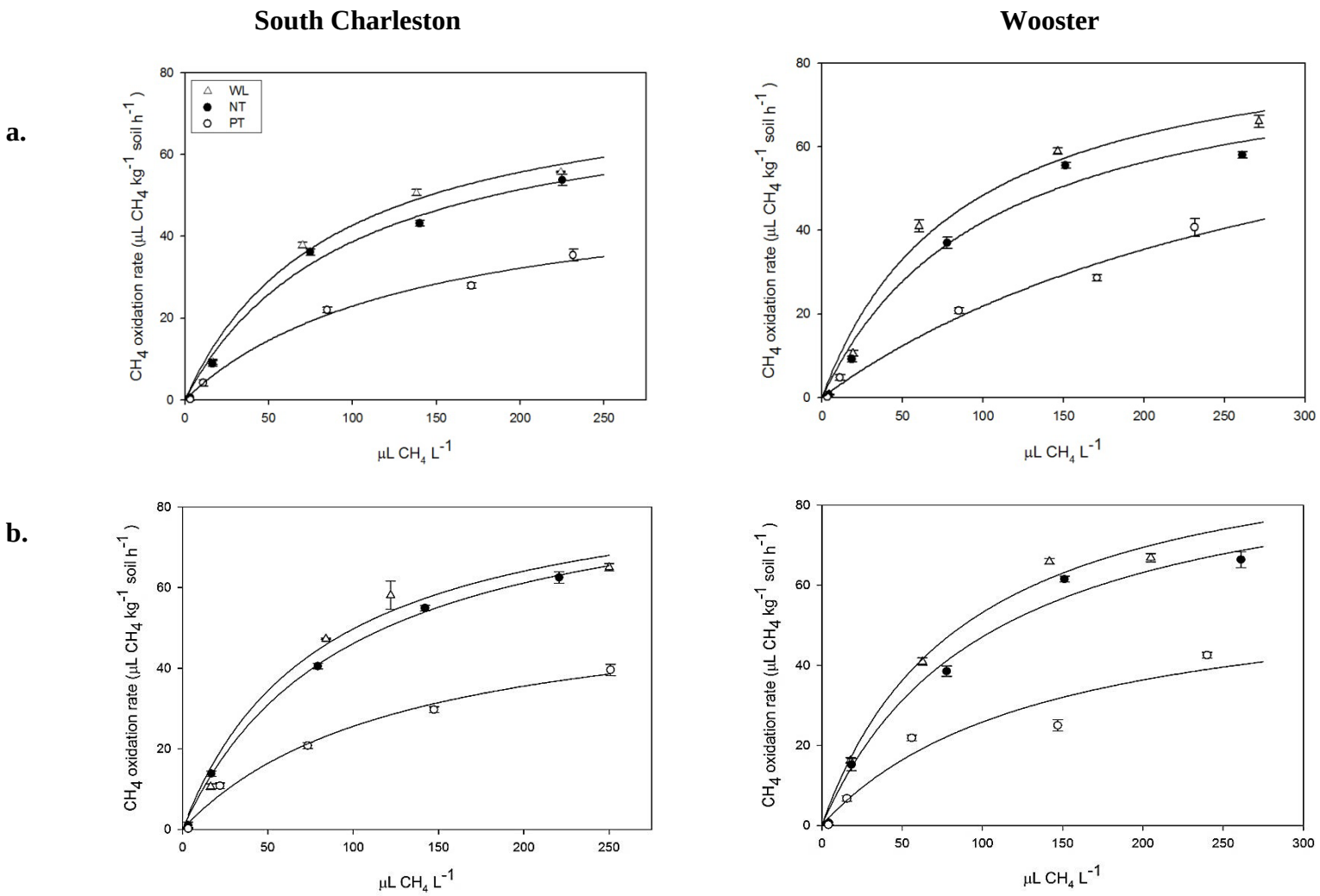


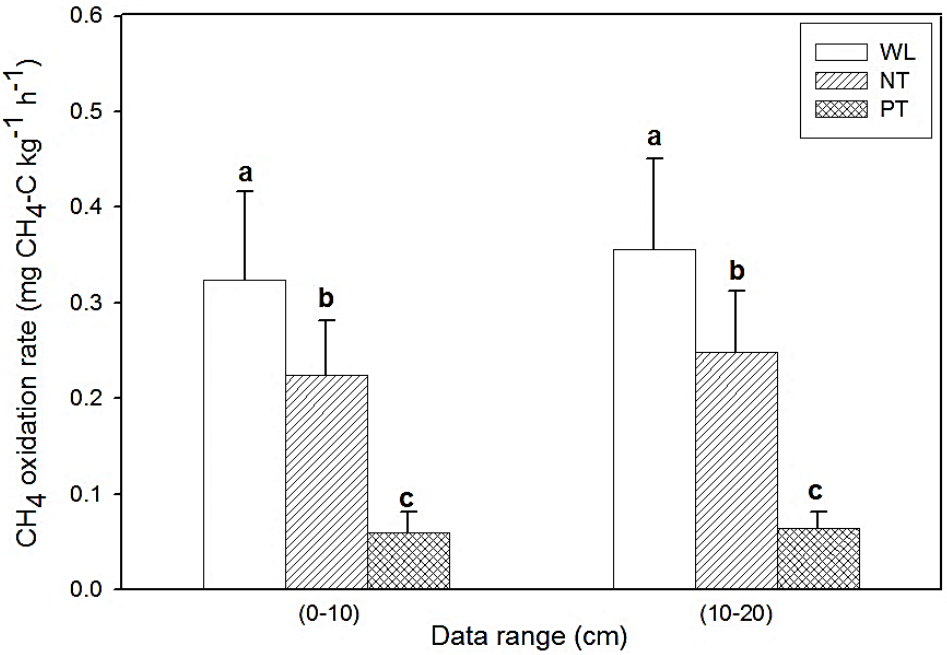
Table 10. Kinetic parameters of CH_4 oxidation in soils in relation to land-use and tillage practices. Values are mean of two replications with standard deviation in parentheses. For a given soil depth, values in a column are significantly different ($p < 0.05$) if they are followed by different letters. Units: V_{max} (μg CH_4-C kg^{-1} h^{-1}), K_m (μL L^{-1}) and Th (μL L^{-1})

	South Charleston			Wooster		
	V_{max}	K_m	Th†	V_{max}	K_m	Th
(0-10)						
WL	43 (0.6)**a***	86.5 (5)**b**	–	48.5 (0.5)**a**	88.9 (3)**b**	–
NT	41.2 (0.5)**b**	98.5 (1)**b**	–	46.2 (0.3)**a**	103.8 (7)**b**	–
PT	29.1 (0.3)**c**	141.7 (6)**a**	–	32.7 (2)**b**	134.9 (4)**a**	–
(10-20)						
WL	48.5 (0.3)**a**	79.5 (8)**c**	0.5**b**	54 (0.1)**a**	88.6 (3)**b**	0.5**b**
NT	46.2 (0.6)**a**	96.8 (2)**b**	0.6**b**	51.8 (0.6)**a**	103.7 (1)**b**	0.5**b**
PT	32.7 (0.7)**b**	127.8 (2)**a**	2.8**a**	32.8 (2.2)**b**	137.4 (10)**a**	2.7**a**

† Sieved soils from the 0-10 cm layer were not incubated for a period long enough for determination of Th. Standard errors for Th are not reported because values are < 0.1.

Fig 11. Rate of CH_4 oxidation in soils from the a) South Charleston and b) Wooster sites in relation to land-use and tillage practices. Vertical bar represents standard deviation of mean of two replicates. Bars are labeled with different letters to indicates significant difference ($p < 0.05$).

a.



b.

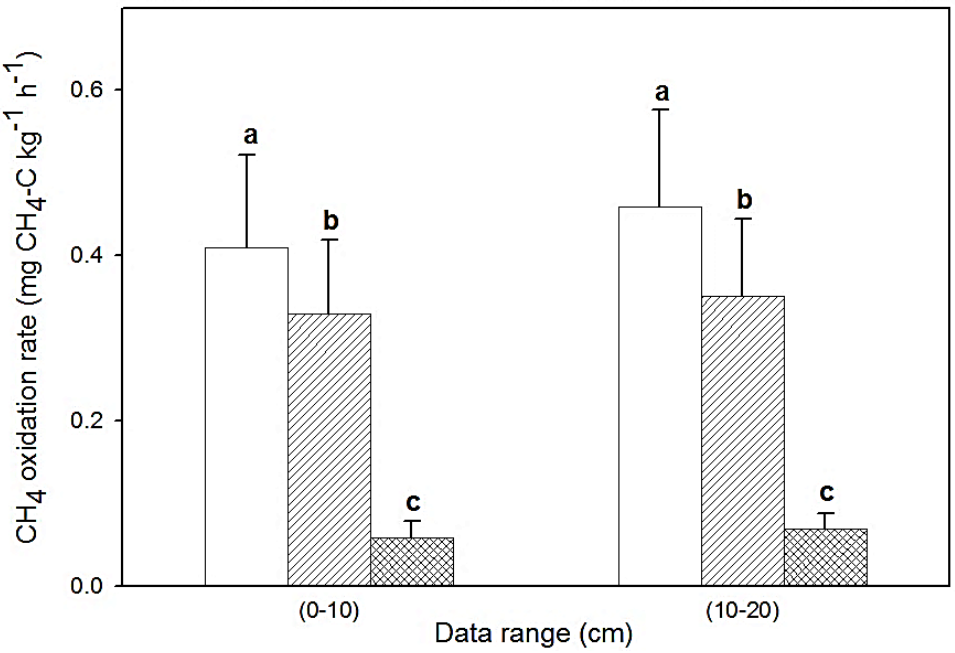


Table 11. Temporal variation in CH_4 oxidation (μg CH_4 kg^{-1} soil h^{-1}) at the a) South Charleston and b) Wooster sites. Soil samples were collected in June and November 2012. Values in parentheses are mean of two replications. Incubation was carried out at near ambient (~ 3 μL CH_4 L^{-1}) CH_4 concentration.

a.

South Charleston

	WL		NT		PT	
	June	**Nov**	**June**	**Nov**	**June**	**Nov**
(0-10)	0.32 (0.02)	0.30 (0.04)	0.22 (0.01)	0.21 (0.02)	0.06 (0.02)	0.05 (0.02)
(10-20)	0.36 (0.00)	0.31 (0.03)	0.25 (0.01)	0.23 (0.03)	0.07 (0.00)	0.06 (0.02)

b.

Wooster

	WL		NT		PT	
	June	**Nov**	**June**	**Nov**	**June**	**Nov**
(0-10)	0.41 (0.01)	0.39 (0.02)	0.33 (0.01)	0.28 (0.02)	0.07 (0.02)	0.06 (0.01)
(10-20)	0.46 (0.02)	0.43 (0.030	0.35 (0.00)	0.34 (0.02)	0.08 (0.01)	0.06 (0.00)

Fig 12. Methane oxidation rate in intact soil core versus sieved soils. Results for the surface (0-10 cm) and subsurface (10-20 cm) soil layers are reported in the top and bottom graphs, respectively. For each set of graphs, data are ported for woodlot (left), no-till (center) and plow till (right). Note the difference in scale for the PT results. Vertical bars represent standard deviation of mean of two replications. The percent value on top of a bar represents CH_4 oxidation in intact core expressed as a % of CH_4 oxidation in sieved soils. Abbreviations: S.C = South Charleston; W = Wooster; WL = woodlot; NT = no-till; PT = plow till

a.

b.

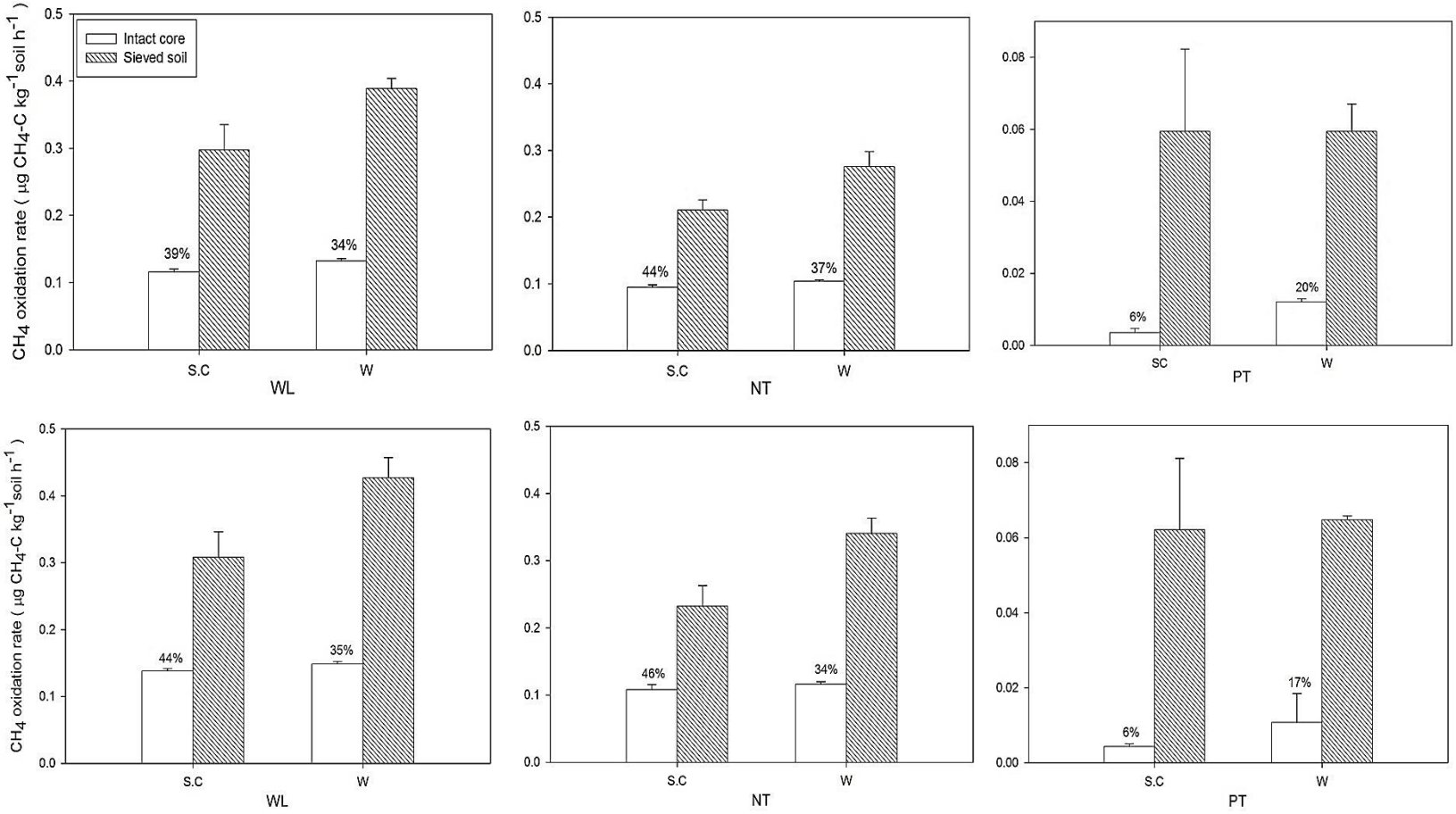
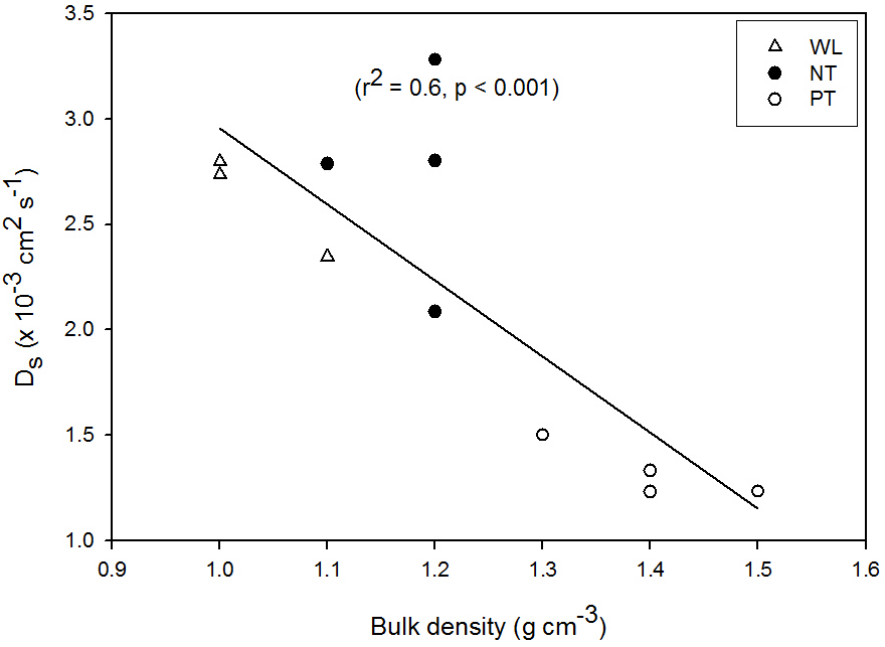


Fig 13. Relationships between bulk density with a) diffusivity and b) CH_4 oxidation rate. Each data point is the mean of two replicates. Results for both study sites and soil depths (0-10, 10-20 cm) are included in each graph.

a.



b.

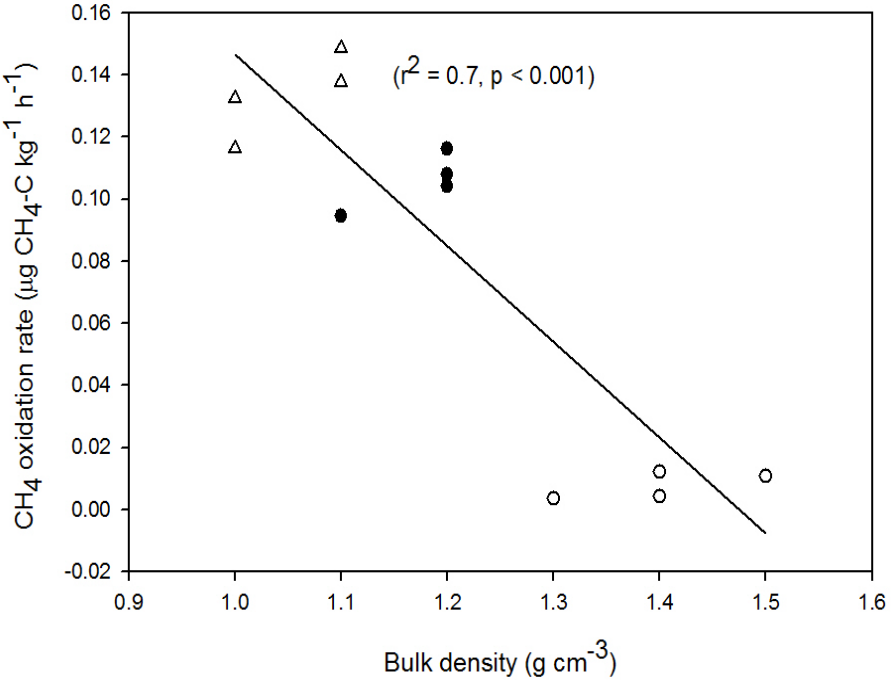
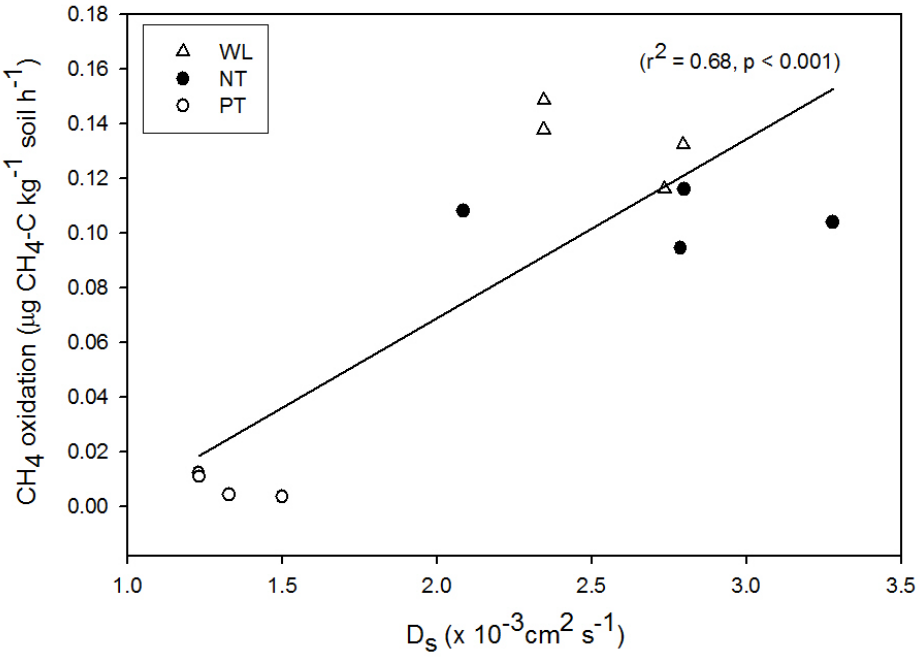


Fig 14. CH_4 oxidation rates in soil intact cores in relation to diffusivity. Each point is the mean of two replication for rates of CH_4 oxidation and three replications for diffusivity (D_s). Results for both study sites and soil depths (0-10, 10-20 cm) are included in the graph.



DISCUSSION

Tillage and Land use effects on CH_4 oxidation in surface soils

Among terrestrial landscapes, grassland and forest soils have generally exhibited the highest capacity to oxidize CH_4. Results of the present study confirm this widely reported observation (Lessard et al., 1994; Ambus and Christensen, 1995; Dobbie et al., 1996). However, the conversion of these natural ecosystems to croplands has generally resulted in a rapid decline of that capacity. Two factors have been proposed to explain the reduction in CH_4 consumption with land use conversion. The first factor includes disturbance of the original soil structure by tillage operations and the resulting loss in ecological niches suitable for methanotrophs (Willison et al., 1995). According to Conrad (1996), oxidation of CH_4 occurs in soil crumbs or in sand grains with biofilms that can offer some protection to methanotrophs from disturbance. This center of methanotrophic activity can easily be destroyed by plowing when forests and or grasslands are converted into croplands.

Application of N-fertilizer is another factor thought to contribute to the low CH_4 oxidation in agricultural soils (Steudler et al., 1989; Adamsen and King 1993; Castro et al., 1994). The effect of NO_3^- has been ascribed to the osmotic stress imposed on methanotrophic bacteria by high NO_3^- concentration in soil solution (Dunfield and Knowles, 1995). In accord with that view, negative relationships between CH_4 oxidation rate and NO_3^- concentration in soils were found in the present study; weak negligible relationship (r^2 =0.15, $p > 0.1$, Fig. 5a) with soils from the South Charleston site and moderate relationship ($r^2 = 0.64$, $p > 0.05$, Fig. 5b) with soil samples from Wooster. The negative effect of NO_3^- on CH_4 oxidation has previously been reported when soil NO_3^-

concentration is in excess of 40 mg NO_3^--N kg^{-1} (Hutsch, 1998a). Since NO_3^- concentration (mean: 34 mg NO_3^- kg^{-1}, Table 4) in the soil samples incubated in this study was below the minimum concentration of NO_3^- required for osmotic effect, that may explain the limited effect of NO_3^- observed in this study.

The decline in CH_4 uptake rates in croplands has also been associated with the inhibitory effect of NH_4^+ fertilization on CH_4 monooxygenase enzyme (MMO) (Mosier et al., 1991; Hutsch et al. 1993; Hutsch et al., 1996; Hutsch 1998a). Immediate, short term effect is usually explained as the competitive inhibition of MMO by NH_4^+ (Adam and King, 1993; Bronson and Mosier, 1994; Dunfield and Knowles, 1995). Long term effect is probably due to repeated applications of NH_4^+-based fertilizer which, in the long run, can cause change in the ecology and composition of soil methanotrophic community (Adam and King 1993; Gulledge et al., 1997). Based on these considerations and the results of several past investigations (King and Schnell, 1994; Hutsch et al., 1993; Hutsch et al., 1996), negative relationships between NH_4^+ concentration and CH_4 oxidation were expected. This expectation was met in the case of the Wooster soils ($r^2 = 0.3$, $p > 0.1$; Fig. 4b). For the South Charleston soils however, the opposite was observed ($r^2 = 0.52$, $p > 0.1$; Fig. 4a). Soils from the South Charleston site have higher clay content (Table 1), and have higher CEC (122-105 mmol/kg) than the silty-loam soil from Wooster (106-76 mmol/kg; Mahboubi and Lal, 1993). It is well known that NH_4^+ ions participate in cation exchange phenomena in soils (Nommik and Vahtras, 1982) and, as a result of its retention on the soil exchange complex, there could be less interaction between NH_4^+ ions in soil solution and the monoxygenase (MMO) enzyme. Therefore, the actual concentration of NH_4^+ in the soil solution may be much lower than suggested by the total

concentration, and this mechanism could thus mitigate the impact of NH_4^+ on CH_4 oxidation in clay-rich soils such as those found at the South Charleston site. As reported in several other studies (Lessard et al., 1994; Ambus and Christensen, 1995; Dobbie et al., 1996), NH_4^+ content in the woodlot soils were considerably higher than in the cropland soils (Table 4). Therefore, the significantly higher rate of CH_4 oxidation in the forest soils suggests that NH_4^+ availability was not a primary factor controlling CH_4 dynamics at the study sites. Higher NH_4^+ concentration in the forest soils is likely the result of more rapid decomposition of leaf litter and greater mineralization of soil organic matter as suggested by basal soil respiration measurements (Table 8). The C/N ratios also indicate relatively higher C quality in organic matter in the forest soils (Table 2 and 3). All these factors indicate greater availability of organic C in forest soils, and this may stimulate the activity of soil methanotrophs (Conrad, 1984). These considerations suggest that NH_4^+ concentration may not be the only factor that control CH_4 oxidation, other soil variables must also be considered.

It has been suggested that the CH_4 oxidation capacity of upland soils can be restored with cessation of tillage disturbance. Numerous studies (Dobbie and Smith, 1996; Prieme et al., 1997; Hutsch, 1998) have shown restoration of activity, but this generally occurs at a very slow rate. The slow recovery has been attributed to extreme sensitivity to disturbance of the methanotrophs that can grow at the low CH_4 concentration typically found in upland soils (King, 1997; Menyailo et al., 2008). The slow recovery may also be due to the slow restoration (over several decades) of the original soil environment for methanotrophs (Prieme et al., 1997; Hutsch 1998; Regina et al., 2007). Suwanwaree and Robertson (2005) argued that the slow recovery of CH_4

oxidation in fertilized agricultural soils can be associated to alterations in the soil microbial community structure and to soil organic matter quality - both of these soil properties evolve very slowly with time. Results of several studies have documented the slow recovery of CH_4 oxidation in disturbed soils (Jacinthe and Lal, 2005; Suwanwaree and Robertson, 2005; Mosier et al. 2006). Mosier et al. (2006) found no effect of tillage on CH_4 oxidation after 3 years of NT adoption in a Colorado irrigated cropland. Jacinthe and Lal (2005) reported similar results for cropland in Central Ohio after 8 years of NT. However, in the present study, a significant effect of NT was observed on both the biological and physical soil parameters linked to CH_4 consumption. Overall, CH_4 oxidation was 5-fold greater in NT soils than in PT soils after 50 years of NT practice (Fig. 11). Regardless of the study sites, CH_4 oxidation in NT soils was 66-80 % of the level in adjacent forest soils (Fig. 11). These results suggest that duration of NT practice is an essential factor in considering the benefits of NT to CH_4 dynamics in soils. While no significant effect is generally noted in the first decade of NT adoption (Jacinthe and Lal, 2005; Mosier et al. 2006), the present study shows that, after 5 decades of NT practice, CH_4 oxidation potential of soils is approaching the level in forest soils. This corroborated the proposition made in several past reports that, several decades without disturbance might be needed to restore the CH_4 oxidation capacity of cultivated soils (Prieme et al., 1997; Sitaula et al., 2000; Jacinthe and Lal, 2004).

Regardless of the soil depths and study sites, SOC, basal soil respiration and MBC were higher in NT soils compared to PT soils, and were close to the level measured in adjacent forest soils (Fig. 3). Strong correlation was also found between size of microbial population (MBC) and CH_4 consumption rate (Table 9). This suggests that

higher C content and availability in NT soils compared to PT soils may have favored the development of larger population of soil microbes including methanotrophs. This observation supports the hypothesis that, in the absence of soil disturbance for a long time, CH_4 oxidation can increase due to development of a larger and more active population of methanotrophs in NT compared to PT soils.

No-till adoption also affects the vertical distribution of methanotrophic activities in soil profiles. In the PT plots, there was no clear change in CH_4 oxidation between the surface and subsurface soil layers (Fig. 11). Since the top 30 cm soil layer is overturned and mixed by an annual plowing, no distinct zone of CH_4 oxidation maximum existed in the PT soil profile. However, clear zonation of activity was observed in NT plots. CH_4 oxidation rate was higher in the subsurface (10-20 cm) layer than in the surface (0-10 cm) layers in the NT plots and woodlots. NH_4^+concentration tends to be higher in the surface soils than in the subsurface soils (Table 3), and since NH_4^+ could be inhibitory to CH_4 oxidation, this distribution may have caused a greater suppression of methanotrophic activities in the surface than in the subsurface soil layers. Further, soil water content fluctuates rapidly in the top soil layer, making it a less favorable environment for methanotrophs than the soil layers just below (Schnell and King, 1996). This may have led to greater population size in subsurface layer where water stress is minimal.

CH_4 oxidation kinetics as affected by tillage

In the present study, clear distinction in CH_4 oxidation activities were observed between the soil samples from NT and PT practice. V_{max} values were generally in the order: WL ≥ NT > PT soils. This ranking is consistent with the results of Bender and

Conrad (1992), and Dunfield and Knowles (1995) who also reported higher V_{max} values for forest soils compared to PT soils. Consistent with the subsurface maximum observed for oxidation rate (Fig. 11), slightly greater activity was generally observed in the 10-20 cm than in the 0-10 cm layer, though difference was not statistically significant (Fig. 12 and Table 10). Regardless of the study sites and depths, V_{max} value was on average 1.5 fold lower in the PT than in NT soils (Table 10). The low methanotrophic activity in PT soils is probably due to a decline in the biomass of the active methanotrophs with chronic soil disturbance (Saari et al., 2004; Menyailo et al., 2008).

Affinity of methanotrophs for CH_4 (K_m) followed the order: WL < NT < PT (Table 10) in soils from both sites. K_m values for all soil samples were within the range reported for upland soils under various types of land use (20-60 μL CH_4 L^{-1} - Bender and Conrad, 1992; Saari et al., 2004 μL CH_4 L^{-1}, ~ 200 μL - Dunfield and Knowles, 1995; Conrad, 1996). The same was true for the measured threshold values (Th) in comparison to those (0.2-2.7 μLCH_4 L^{-1}) previously reported by Bender and Conrad (1992).

It has been also been demonstrated that ammonia-oxidizing bacteria can oxidize CH_4 as an alternative substrate for ammonia monooxygenase (Suzuki et al., 1976; Hyman and Wood, 1983; Jones and Morita, 1983; Ward, 1987). Methane oxidation by nitrifiers has mostly been detected in field and laboratory incubation studies conducted at elevated (> 100 μL CH_4 L^{-1}) CH_4 concentration (Goldman et al., 1995; Chan and Parkin, 2001). Further, K_m values for CH_4 oxidation by nitrifiers are typically > 6,600 μL CH_4 L^{-1} (Conrad, 1996). Therefore, in the soils tested in the present study, CH_4 oxidation has probably been carried out predominantly by methanotrophs.

In general, measured K_m values (127-141 μL CH_4 L^{-1}) for the PT soils were significantly higher than that for the NT (96-104 μL CH_4 L^{-1}) soils (Table 10), and were in the same range (189 μL CH_4 L^{-1}) reported by Dunfield and Knowles (1995) for agricultural soils. Despite the fact that soil samples came from the experimental plots under similar management practice (except tillage) and receiving similar amounts of fertilizer, the higher K_m values in PT soils suggests a possible impact of periodic tillage disturbance on growth conditions and affinity of methanotrophs for CH_4 (Saari et al., 2004). In addition, significantly higher Th values in PT soils (2.8 μL CH_4 L^{-1} versus 0.5 μL CH_4 L^{-1} in NT) also suggest a loss in the vitality of methanotrophs under PT and in their ability to oxidize atmospheric CH_4 (~1.7 μL CH_4 L^{-1}). However under NT, methanotrophs appeared to have developed into a more stable community approaching the activity measured in the forest soils. Derived kinetic parameters (Table 10) for the NT soils (V_{max}: 43-48 μg CH_4-C kg^{-1}, K_m: 97-104 μL CH_4 L^{-1}, Th: 0.5 μL CH_4 L^{-1}) were similar to those obtained for WL soils (V_{max}: 46-51 μg CH_4-C kg^{-1}; K_m: 79-89 μL CH_4 L^{-1}; Th: 0.7 μL CH_4 L^{-1}). These results suggest that, after about 5 decades without disturbance, the biological conditions of NT soils may have improved to a level similar to that of a forest soils. Overall, the observed trend in kinetic parameters (K_m and Th) could be a reflection of change in either the composition or the activity of the methanotrophic community in NT soils (Chan and Parkin, 2001). Although microbial community analysis will be needed, these results (V_{max}, K_m, Th) provide strong support for the hypothesis that a large and active population of methanotrophs evolve under long term NT due to the absence of physical soil disturbance. Using molecular techniques, Singh et al. (2007) showed that afforestation of pasture can cause increment in CH_4 oxidation capacity due

to alteration in the community structure of methanotrophs. In contrast, Menyailo et al. (2008) observed little change in the composition of high affinity methanotrophs between natural grassland, and afforested land which was once grassland. The reduction in oxidation capacity in artificially afforested soils as compared to natural grassland was attributed predominantly to the decline in biomass and cell specific activity of methanotrophs.

CH_4 transport as affected by tillage and drainage characteristic

Methane uptake in soils is a substrate-dependent process. Transport of CH_4 to the sites of microbial oxidation can be controlled by soil gas diffusivity (Dorr et al., 1993; Ball et al., 1997b) - a soil physical property that varies with soil texture, soil moisture and land management. Ball et al. (1997) measured higher gas diffusivity in coarse-textured than in fine-textured soils. Others (Kruse et al., 1996; Boeckx et al., 1997; Saari et al., 1997; Kravchenko et al., 2000) showed a similar link between soil texture and CH_4 transport. In the present study, soil texture seemed to have only a marginal effect. Although soil texture at both sites is classified as loamy, the higher clay content (Table 1) in the Crosby soil at the South Charleston site may have contributed to the lower CH_4-diffusivity in the South Charleston soil cores compared to the Wooster cores. However, difference between the sites with regard to diffusivity was not statistically different (Table 7).

To examine the impact of transport processes on CH_4 oxidation, incubation was conducted using intact cores and sieved soil samples at near ambient (~ 3 µL CH_4 L^{-1}) CH_4 concentration. Methane oxidation was significantly higher (3-4 fold) in sieved soils

than in intact cores, indicating diffusion restriction on CH_4 transport to the site of oxidation inside the soil cores (Fig. 13). The restriction was significantly higher in PT cores (oxidation in intact cores was 6-20 % of that in sieved soils) than in NT and WL cores (oxidation in intact cores was 34-44 % of that in sieved soils) suggesting greater diffusion restriction under PT, especially in poorly-drained soils. Jacinthe and Lal (2006) also found a similar trend; in a study using silty loam soil and clay loam soils, reported CH_4 oxidation rates were 7-10 fold lower with soil cores than with sieved soil samples. In contrast, Hutsch (1998) found that in sandy soil, CH_4 oxidation rate was higher in intact cores than in sieved soils. To interpret these contradictory results, Jacinthe and Lal (2006) proposed two possible scenarios which seemed plausible for this experiment as well. In contrast to the silt loam examined in the present research, the study of Hutsch (1998) was conducted with sandy soil. The diffusion of CH_4 from a jar headspace to the site of oxidation activity is probably less restrictive in the sandy soils used by Hutsch (1998) than in the silty loam soils used in this experiment. Moreover, the present study was carried out using < 6.3 mm soil aggregate (sieve opening, 6.3 mm). Therefore, microsites of active methanotrophy were probably minimally disturbed by the soil sieving process. In contrast, the use of $\leq$ 5 mm sieve for the sandy soil by Hutsch (1998) might have led to severe disruption of these microsites, resulting in reduced CH_4 oxidation.

Tillage disrupts soil aggregates (Mahoubi and Lal, 1998), and the use of heavy machinery on cultivated land has also been blamed for soil compaction. Adoption of NT improves soil stability and soil aggregation (Mahoubi and Lal, 1998). In well aggregated soils, inter aggregate macro-pores are likely to be present, forming a continuous network for the passage of soil water and air (Hillel, 1998). In light of the positive impact of NT

on soil aggregation, and the positive relationship between aggregation and soil porosity (Lal et al., 1994; Ball et al., 1997b), it was hypothesized that NT soils will have greater CH_4 diffusivity due to improved soil aggregation and greater porosity. The study results are in agreement with this hypothesis. Soil-CH_4 diffusivity values were within the same range as reported in a previous study (10^{-3} cm^2 s^{-1}, Grundmann and Chalamet, 1987) and were significantly higher in NT and WL cores than in PT cores. Air-filled porosity was also greater in NT (~ 0.37 cm^3 cm^{-3}) and WL cores than in PT (~ 0.28 cm^3 cm^{-1}) (Fig. 7). This suggests that not only soils under NT and WL have large volume of air-filled pores but also these pores are presumably continuous. This interpretation is in accord with previous reports of greater interconnection of soil pores under NT compared to PT (Logsdon et al., 1993; Frede et al., 1994; Reynolds et al., 1995, 2000; Tebrugge and During, 1999; Cameira et al., 2003). According to Blackwell (1990), total soil porosity in forest soils is likely dominated by macro-pores which are not only of greater size but also are well-interconnected. These wide pores are favorable to methanotrophic activity and enhanced CH_4 oxidation in soils (Bender and Conrad, 1994). A strong relationship (r^2= 0.64, $P < 0.01$) between diffusivity and CH_4 oxidation (μg CH_4-C kg^{-1} soil h^{-1}; Fig. 14a) was observed. Ball et al. (1997) found a similar strong relationship ($r^2 = 0.92$) between methane uptake (mg m^2 d^{-1}) and relative diffusivity. These observations suggest that soil gas transport properties improves with NT adoption, and this in turns can have a positive impact on CH_4 uptake (Dorr et al., 1993; Ball et al., 1997).

Several soil-gas diffusion models (Penman, 1940; Troeh et al, 1982; Moldrup et al., 1996; Ridgwell et al., 1999) suggest exponential relationships between air-filled porosity and diffusivity. But in the present study, a linear relationship ($r^2 = 0.8$, $p <$

0.001) was found between these variables. This could be because the porosity values in the present study were in the range of 20-60% (> 0.1 cm^3 cm^{-3}) - a range where the relationship with gas diffusivity is generally linear (Troeh et al., 1982; Ball et al., 1997; Jabro et al., 2012).

NT can sometimes lead to soil compaction due to increase in soil bulk density, but this outcome depends upon antecedent soil condition, soil texture, and sampling location relative to wheel tracks left by farm machinery. For a clay loam soil, Gantzer and Blake (1978) reported higher bulk density and lower total porosity under NT than under PT. Others have reported similar effects of NT on soil porosity and reduced macropore volume (Starr, 1990; Ankeny et al., 1990; Culley et al., 1987a, b). However, Shear and Moschler (1969), and Lal et al. (1994) found no significant effect of tillage on bulk density. These results highlight the difficulty in restoring soil structure after the cessation of tillage disturbance. Mapa (1995) noted that, after 12 years of reforestation in Sri Lanka, soil porosity was still far from its maximum. In the present study, it was hypothesized that, gaseous transport will be more restricted in NT plots due to increase in bulk density, especially in the fine-textured and poorly drained Crosby soil at the South Charleston site. Contrary to that hypothesis, no significant effect of soil type on bulk density and CH_4-diffusivity was found. However, the effect of tillage on both parameters was significant (Table 6 and 7). Strong negative relationships between bulk density and diffusivity ($r^2 = 0.6$, $P < 0.001$, Fig. 13a); bulk density and methane oxidation rates ($r^2 = 0.7$, $P < 0.001$) were observed (Fig. 13b). MacDonald et al. (1996) found a similar trend between bulk density and methane oxidation in agricultural soils. Hansen et al. (1993) reported a 52 % reduction in CH_4 oxidation rates following increase in the bulk density

due to cultivation. Thus, apart from its influence on soil aggregation, tillage operations can also influence gaseous transport owing to its impact on bulk density.

Soil moisture content varied significantly with respect to the site and tillage practices (Table 4). Soil moisture content was significantly higher in NT than in PT soils. Despite higher soil moisture, CH_4-diffusivity in NT soils was greater than in PT soils. As discussed earlier, NT practice leads to larger volume of macro-pores compared to PT practice (Lal et al., 1994; Buczko et al., 2006; Kumar et al., 2012). Although micropores may have been occupied by water, the macro-pores in NT soils were probably not filled up. Presumably, these macropores may have continued to provide a pathway for active gaseous transport even at relatively high moisture content. Overall, these findings underscore the beneficial effect of NT farming practice on CH_4 transport compared to PT.

CONCLUSIONS

Past studies have shown a significant reduction in CH_4 oxidation in soils when undisturbed natural ecosystems (forests, grasslands) are converted to agricultural land use. It has been suggested that, due to the absence of physical land disturbance, NT farming could help restore the CH_4 sink capacity of cultivated soils, but few studies have examined the validity of that suggestion. Most past studies have only investigated soils under NT for less than two decades when methanotrophic community was far from full restoration. In addition, the comparison of NT and PT practices is often confounded by other factors such as soil type, climate, fertilizer management and crop rotation. The present study was designed to address this information gap, and with consideration of the confounding factors listed above. In this study, CH_4 oxidation activity was measured in arable soils where tillage disturbance had ceased for five decades. In addition, the soils tested were from adjacent experimental plots under similar management. By controlling for all these other factors, tillage practice was the only experimental variable in the study.

Results showed a distinct effect of tillage on CH_4 oxidation. Both the CH_4 oxidation capacity (measured at near ambient CH_4) and oxidation potential (measured at elevated CH_4) were significantly greater in the NT soils compared to PT. This trend was consistent regardless of sampling season and the natural drainage characteristics (well-drained vs. poorly-drained) of the soils tested. CH_4 oxidation rates measured with intact cores were significantly lower than in sieved soils supporting the contention that diffusion could restrict CH_4 oxidation. Mean CH_4 oxidation rate in NT and PT soils were 66-80 % and 10-16 %, respectively of the level recorded in adjacent forest soils. Likewise, the maximum oxidation rate (V_{max}) was on average 1.5 times higher in NT (43-

48 µg CH_4 L^{-1} kg^{-1} h^{-1}) soils than in the PT (29-32 µg CH_4 L^{-1} kg^{-1} h^{-1}). Conversely, the half saturation constant (K_m) and threshold for CH_4 oxidation (Th) - parameters expressing the affinity between an enzyme and its substrate - were lower in NT than PT soils. These observations suggest the evolution, in long-term NT soils, of a methanotrophic community with greater affinity, activity and ability to oxidize atmospheric CH_4.

Tillage practice also had a significant impact on CH_4 transport. Diffusivity in NT (2-3 x 10^{-3} cm^2 s^{-1}) cores were greater compared to PT cores (1.5 x 10^{-3} cm^2 s^{-1}). Improved soil structure and soil aggregation in NT plots compared to PT plots probably have led to the development of larger number of macro-pores conducive to CH_4 transport in the NT cores. No effect or a very limited effect of soil type on gaseous transport was found. These results indicate that, long term adoption of NT farming can improve both the soil biology, and the transport properties suitable for CH_4 uptake. Therefore, NT farming is a better soil management option compared to conventional farming (PT) in mitigating CH_4 emission associated with agriculture.

LIMITATIONS

Although this research has reached its aim, it is not without some limitations. First, one must recognize that laboratory-based studies can only provide an indication of the potential but not the actual intensity of a soil process. Methane incubation experiments conducted under laboratory-controlled conditions may not necessarily represent actual field conditions.

The year 2012 was the 13th driest year on record for Ohio. This may have affected soil moisture regime, and thus the population of soil methanotrophs in that year. A possible influence of weather conditions on CH_4 oxidation capacity of soils cannot be ruled out. It would therefore be of interest to conduct a similar assessment of the oxidation capacity of soils during a year with near normal precipitation.

Clear differences were observed between NT and PT soils with respect to K_m and threshold (Th) for CH_4 oxidation. These observations are indicative of change in the composition of soil methanotrophs, but there remains some uncertainty with this interpretation. Therefore, the next possible research avenue could be the use of molecular techniques such as polymerase chain reaction (PCR) and phospholipid fatty acid (PLFA), to characterize the community composition and biomass of methanotrophs in soils under PT in comparison to long-term NT practices. Such investigations could validate the inference made in the present study.

APPENDICES

Appendix A. Methane concentration in jar headspace during incubation of soils from different land-use and tillage practices. Soil samples are from the South Charleston site. "I" and "II" are the Jar replicates. Abbreviations: WL = woodlot; NT = no-till and PT = plow till.

Tillage /land-use	Duration of Incubation (h)						
	0	46.02	70.43	92.68	144.02	165	215.45
	Concentration of CH_4 (ppm)						
WL (0-10 cm)							
I	3.37	2.89	2.66	2.47	2.08	1.94	1.64
	19.56	12.09	9.37	7.43	4.34	3.49	2.06
	60.10	42.36	35.19	29.71	20.11	17.15	11.69
	146.02	112.12	97.46	85.78	63.88	56.64	42.40
	271.32	228.63	208.78	192.20	158.78	146.86	121.73
II	4.10	3.60	3.36	3.15	2.72	2.57	2.22
	19.15	11.83	9.16	7.26	4.24	3.40	2.01
	61.00	43.18	35.94	30.41	20.68	17.67	12.10
	146.09	112.23	97.58	85.90	64.01	56.76	42.51
	271.35	227.61	207.34	190.45	156.53	144.48	119.15
WL (10-20)							
I	3.21	2.76	2.55	2.37	2.00	1.87	1.59
	17.96	10.83	8.28	6.48	3.68	2.92	1.68
	62.1	39.19	30.71	24.58	14.71	11.93	7.20
	141.02	97.14	79.71	66.57	43.92	37.05	24.62
	205.1	167.50	150.45	136.42	108.83	99.24	79.48
II	3.21	2.7	2.46	2.26	1.86	1.72	1.23
	17.39	10.91	8.52	6.80	4.04	3.27	1.96
	62.59	40.24	31.83	25.71	15.71	12.84	7.91
	141.93	97.95	80.45	67.24	44.46	37.54	25.00
	205.3	168.29	151.44	137.56	110.20	100.65	80.94
NT (0-10)							
I	3.41	3.01	2.90	2.73	2.44	2.30	2.08
	18.39	12.15	9.76	7.99	5.03	4.17	2.65
	77.75	61.43	54.21	48.37	37.19	33.40	25.80
	151.11	39.78	19.60	10.28	2.32	1.26	0.29
	264.15	225.89	207.90	192.75	161.88	150.73	126.97
II	4.02	3.42	3.16	2.93	2.46	2.29	1.93
	17.93	17.94	17.95	17.96	17.97	17.98	17.99
	76.89	60.78	53.65	47.88	36.83	33.09	25.57
	151.02	130.34	120.55	112.26	95.25	89.07	75.79
	261.70	223.90	206.12	191.14	160.61	149.58	126.07

NT(10-20)							
I	3.29	2.94	2.77	2.62	2.32	2.20	1.94
	16.98	8.92	6.33	4.64	2.26	1.69	0.83
	77.73	52.08	42.12	34.71	22.20	18.50	11.93
	142.21	104.96	89.34	77.14	54.97	47.86	34.31
	220.78	177.84	158.56	142.82	112.20	101.66	80.20
II	3.37	2.61	2.29	2.05	1.59	1.45	1.16
	17.01	8.95	6.36	4.66	2.28	1.70	0.84
	82.77	55.72	45.17	37.30	23.99	20.03	12.98
	144.51	106.85	91.04	78.68	56.18	48.96	35.16
	219.27	175.73	156.26	140.40	109.68	99.15	77.79
PT (0-10)							
I	3.16	3.01	2.94	2.89	2.8	2.76	2.71
	11.03	8.72	7.70	6.88	5.29	4.75	3.68
	84.87	66.20	58.02	51.45	38.99	34.82	26.51
	170.80	145.39	133.48	123.48	103.17	95.87	80.35
	231.60	199.89	184.87	172.16	146.08	136.59	116.23
II	3.41	3.29	3.23	3.18	3.07	3.03	2.95
	14.23	11.26	9.94	8.89	6.84	6.14	4.75
	72.62	57.14	50.31	44.81	34.29	30.74	23.64
	129.00	109.91	100.96	93.44	78.15	72.65	60.95
	203.13	176.20	163.40	152.55	130.17	122.00	104.39
PT(10-20)							
I	3.50	3.36	3.29	3.23	3.12	3.08	2.98
	16.00	10.11	7.91	6.33	3.79	3.07	1.86
	73.43	58.58	51.96	46.58	36.20	32.66	25.49
	147.42	123.94	113.04	103.97	85.66	79.14	65.43
	250.86	210.90	192.36	176.88	145.76	134.67	111.35
II	3.42	3.29	3.24	3.18	3.09	3.05	2.96
	16.00	11.13	7.94	6.37	3.72	3.10	1.88
	73.43	58.88	52.37	47.06	36.78	33.26	26.11
	146.42	123.72	113.15	105.30	86.43	80.04	66.55
	248.86	218.7	204.28	191.80	166.03	156.53	135.84

Appendix B. Methane consumption in jar headspace during incubation of soils from different land-use and tillage practices. Soil samples are from the Wooster site. "I" and "II" are the Jar replicates. Abbreviation WL = woodlot; NT = no-till and PT= plow till.

Tillage/land-use	Incubation time (h)						
	0	46.02	70.43	92.68	144	165	215.45
	CH_4 Concentration (ppm)						
Source WL(0-10)							
I	4.08	3.49	3.21	2.98	2.51	2.34	1.98
	19.56	11.74	8.95	6.99	3.95	3.13	1.79
	60.10	34.60	25.81	19.76	10.67	8.30	4.53
	146.02	104.79	87.88	74.85	51.69	44.44	30.89
	271.32	219.93	196.75	177.75	140.63	127.79	101.51
II	4.20	3.71	3.47	3.27	2.85	2.69	2.35
	19.15	13.87	11.70	10.01	6.99	6.03	4.24
	146.09	92.21	72.23	57.83	34.61	28.06	16.94
	146.00	104.13	87.05	73.93	50.71	43.47	30.01
	271.35	220.39	197.37	178.48	141.52	128.72	102.47
WL (10-20)							
I	3.96	3.41	3.01	2.76	2.26	2.08	1.62
	17.96	8.80	6.03	4.27	1.93	1.39	0.64
	62.10	36.56	27.61	21.37	11.84	9.30	5.20
	141.02	96.25	78.60	65.34	42.67	35.85	23.59
	205.10	169.83	153.66	140.26	113.64	104.27	84.79
II	3.96	3.28	2.96	2.70	2.19	2.01	1.63
	17.39	7.75	5.05	3.41	1.38	0.96	0.39
	62.59	35.85	26.68	20.38	10.94	8.49	4.61
	141.93	95.15	76.96	63.43	40.60	33.83	21.83
	205.30	155.05	133.60	116.64	85.28	75.04	55.16

NT (0-10)							
I	3.32	2.93	2.75	2.59	2.25	2.13	1.86
	18.39	12.61	10.33	8.61	5.65	4.76	3.15
	77.75	54.30	44.89	37.74	25.28	21.47	14.48
	151.11	114.65	99.03	86.65	63.68	56.15	41.48
	264.15	222.83	203.61	187.54	155.12	143.55	119.13
II	4.21	3.75	3.52	3.33	2.92	2.77	2.34
	18.13	12.60	10.39	8.72	5.81	4.92	3.31
	76.89	52.38	42.73	35.50	23.13	19.42	12.75
	151.02	113.01	96.90	84.23	60.95	53.41	38.86
	260.62	212.55	190.77	172.87	137.73	125.52	100.41
NT(10-20)							
I	3.35	2.88	2.66	2.47	2.08	1.92	1.63
	18.98	9.97	7.08	5.19	2.53	1.88	0.93
	77.73	51.39	41.27	33.79	21.30	17.63	11.20
	151.21	108.06	90.43	76.87	52.84	45.34	31.37
	261.78	212.32	190.01	171.71	135.94	123.56	98.22
II	3.37	2.96	2.76	2.59	2.24	2.11	1.82
	18.38	8.76	5.91	4.13	1.81	1.29	0.57
	77.77	52.84	43.04	35.70	23.20	19.45	12.73
	151.50	107.28	89.34	75.61	51.44	43.95	30.11
	261.27	210.45	187.64	169.01	132.78	120.31	94.91
PT (0-10)							
I	3.30	3.19	3.13	3.09	3.00	2.97	2.90
	11.03	7.85	6.55	5.56	3.80	3.25	2.24
	84.86	70.93	64.49	59.13	48.40	44.59	36.63
	170.80	149.46	139.25	130.55	112.49	105.85	91.44
	231.60	201.42	187.04	174.83	149.61	140.39	120.46
II	3.18	3.08	3.03	2.99	2.88	2.84	2.75
	11.23	8.45	7.26	6.33	4.61	4.05	2.96
	84.62	68.60	61.38	55.45	43.88	39.88	31.68
	170.00	147.43	136.69	127.59	108.84	102.00	87.25
	231.13	198.66	183.33	170.39	143.91	134.31	113.77

PT(10-20)							
I	3.42	3.29	3.24	3.18	3.09	3.05	2.97
	11.03	7.85	6.55	5.56	3.80	3.25	2.24
	84.87	70.93	64.49	59.13	48.40	44.59	36.63
	170.80	149.46	139.25	130.55	112.49	105.85	91.44
	231.60	201.42	187.04	174.83	149.61	140.39	120.46
II	3.18	3.06	3.01	2.96	2.88	2.84	2.78
	11.23	8.45	7.26	6.33	4.61	4.05	2.96
	84.62	68.60	61.38	55.45	43.88	39.88	31.68
	170.00	147.43	136.69	127.59	108.84	102.00	87.25
	231.13	198.66	183.33	170.39	143.91	134.31	113.77

Appendix C. Methane concentration in the "source jar" and "sink jar" during the diffusion experiment. The soil cores used were extracted from the South Charleston (A) and Wooster (B) experimental plots. I and II are jar the replicates. Abbreviation NT = no-till; WL = woodlot and PT = plow till.

A. South Charleston

Tillage/land-use	Duration of incubation (h)						
	0	16.35	39.83	64.78	70.13	87.48	140.68
	Concentration of CH_4 (ppm)						
Source							
WL (0-10 cm)							
I	24343.0	18256.7	14419.8	12952.1	12793.7	12469.6	12202.8
II	26108.1	20930.5	16866.4	14817.5	14548.8	13928.5	13223.0
WL (10-20)							
I	23623.6	19688.3	15624.1	13575.3	13306.6	12686.3	11980.8
II	23155.8	18713.8	15138.9	13279.4	13030.2	12446.9	11757.8
NT (0-10)							
I	24834.8	19310.3	15377.1	13622.9	13411.7	12949.8	12495.8
II	24834.8	19198.5	15261.5	13547.3	13344.4	12905.2	12485.5
NT (10-20)							
I	25463.9	20376.3	16390.4	14385.8	14123.3	13518.1	12831.7
II	25591.1	21254.0	17463.1	15277.3	14963.0	14192.5	13158.8
PT (0-10)							
I	23861.0	20689.5	17550.0	15437.3	15100.0	14213.9	12765.9
II	25084.4	21705.2	18379.7	16157.8	15804.8	14880.5	13384.2
PT (10-20)							
I	24587.7	22475.4	19419.0	17170.2	16789.3	15747.2	13832.2
II	24343.0	21329.3	18257.5	16114.2	15763.8	14827.7	13224.1
Sink							
WL (0-10)							
I	3.1	6086.3	9923.2	11390.9	11549.3	11873.4	12140.3
II	3.2	5177.6	9241.7	11290.6	11559.3	12179.6	12885.1
WL (10-20)							
I	3.3	3935.3	7999.4	10048.3	10317.0	10937.3	11642.8
II	2.5	4442.0	8016.9	9876.4	10125.6	10708.9	11398.0
NT (0-10)							
I	2.5	5524.5	9457.7	11211.9	11423.1	11885.0	12339.0

II	3.1	5636.2	9573.2	11287.5	11490.4	11929.6	12349.2
NT (10-20)							
I	3.4	4960.5	8946.4	10951.0	11213.5	11818.7	12505.1
II	2.9	4337.1	8128.0	10313.8	10628.1	11398.6	12432.3
PT (0-10)							
I	2.8	3171.5	6311.0	8423.7	8761.0	9647.1	11095.1
II	4	3379.2	6704.7	8926.6	9279.6	10203.9	11700.2
PT (10-20)							
I	3.4	2112.3	5168.7	7417.5	7798.4	8840.5	10755.5
II	3.4	3013.7	6085.5	8228.8	8579.3	9515.3	11119.0

B. Wooster

Tillage/land-use	**Duration of incubation (h)**						
	0	49	74	101	121	145	167
	Concentration of CH_4 (ppm)						
Source							
WL (0-10)							
I	24834.4	16630.0	14826.4	13765.9	13281.0	13024.0	12727.7
II	26108.1	15750.4	14247.2	13565.9	13321.2	13176.8	13114.1
WL (10-20)							
I	23623.6	14543.5	13093.2	12395.9	12131.2	11990.9	11891.7
II	23155.8	14040.9	12684.5	12060.2	11832.7	11696.7	11636.8
NT (0-10)							
I	25336.5	14238.0	13201.6	12842.2	12741.8	12694.5	12678.4
II	24100.8	13507.4	12539.2	12207.7	12116.2	12073.6	12059.3
NT (10-20)							
I	23364.0	13716.9	12893.4	11994.4	11832.1	11744.4	11709.9
II	25591.1	14839.6	13587.5	13091.5	12934.5	12851.8	12820.1
PT (0-10)							
I	22247.8	16192.0	14499.5	13337.7	12925.0	12210.4	11885.0
II	25084.4	18145.2	16236.3	14939.5	14262.0	13698.0	13344.6
PT (10-20)							
I	24587.7	18264.4	16704.0	15083.3	14365.2	13944.4	13339.7
II	28001.1	19215.4	17130.3	15842.8	15226.8	14753.9	14482.3

Sink							
WL (0-10)							
I	3.8	8204.1	10007.6	11068.1	11553.0	11910.1	12706.3
II	2.6	10357.6	11860.9	12542.2	12786.9	12931.3	12994.0
WL (10-20)							
I	3.6	9080.1	10530.3	11227.7	11492.3	11656.6	11731.8
II	3.2	9114.9	10471.3	11095.6	11323.1	11459.1	11519.0
NT (0-10)							
I	2.4	11098.5	12134.9	12494.3	12594.7	12642.0	12758.0
II	3.4	10593.4	11561.6	11893.1	11984.5	12027.2	12041.5
NT (10-20)							
I	2.7	9747.1	10970.6	11669.6	11531.9	11619.6	11654.1
II	4.2	10751.5	12003.6	12499.6	12656.6	12739.3	12771.0
PT (0-10)							
I	3.5	6055.8	7748.3	8910.1	9522.8	10037.4	10362.9
II	3.4	6939.1	8848.0	10144.9	10822.3	11386.4	11739.7
PT (10-20)							
I	3.5	6323.3	8183.7	9904.3	10222.5	10843.3	11247.9
II	2.7	8785.6	10870.7	12158.2	12774.2	13247.1	13518.8

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CURRICULUM VITAE

Prajaya Prajapati

Education

M. S. in Geology, Indiana University , IUPUI — Aug 2011 - Sep 2013

B. S in Forestry Science, Institute of Forestry,
Tribhuvan University, Nepal — March 2005 - March 2009

Honors and Awards

Tribhuwan University meritorious student Scholarship
throughout undergraduate studies — 2005 - 2009

Skills and Abilities

Installation of gas chambers for measuring GHG's flux, Lab analysis of gas samples using Gas Chromatograph (Varion 3800), Lab analysis of water chemistry using Konelab photometric analyzer, Microsoft Word, Excel and PPT, and Sigma Plot

Professional Experience

Biogeochemistry laboratory technician
IUPUI Soil Biogeochemistry Lab, Indianapolis, IN — Aug 2011 - Aug 2013

Forest Survey technician
Institute of forestry, Pokhara, Nepal — March 2005 - Dec 2009

Conference Attended

Diffusion limitation of methane oxidation in soils under
long term no-till management practices — Oct 21, 2012 - Oct 24, 2012

Professional Associations

Member of the Soil Science Society of America,
and American Society of Agronomy — Aug 2011 - Aug 2013

Member of forester association of Nepal — July 2005 - Dec 2010

Self-Help Environment Awareness Camp (SHEAC),
IOF, Pokhara — July 2005 - Dec 2010

Abstracts and Publications

Prajapati, P., and Jacinthe, P.A. (2013). Biological Potential and Diffusion limitation of methane oxidation in long-term NT soil. (Master's degree thesis, on-going).

Prajapati, P., and Awasthi, K. D. (2010). An Assessment of Soil Quality Index and Soil Carbon Sequestration in Different Land Uses- A case study from Nagarkot VDC of Bhaktapur**.**