Understanding the relationships between microbial biomass, enzymes and greenhouse gas efflux in a secondary forest in Missouri

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ABSTRACT

Carbon dioxide (CO_2), nitrous oxide (N_2O) and methane (CH_4) concentrations are increasing at annual rates of 0.5%, 0.75% and 0.75% respectively. Documented research has established links between soil physical and chemical properties and efflux of greenhouse gasses; however a need exists for closer examination of the relationship among soil microbial properties, management practices, and greenhouse gas efflux. This study investigated the relationship between the spatial distribution of greenhouse gases, soil microorganisms and microbial activity within a secondary forest in central Missouri. Laboratory assessments of field samples included determination of gas flux rate, microbial biomass by total organic carbon (TOC) and chloroform fumigation extraction; and enzyme activity by beta-glucosidase assay. Results showed a slight but not significant decrease in CO_2 efflux, and significantly higher efflux of N_2O and CH_4 in 2007 versus 2006. The higher efflux in N_2O and CH_4 may be related to similar changes in some soil biological and thermal properties from 2006 to 2007. For example â-glucosidase activity significantly increased from 228.5 µg PNP g^{-1} soil h^{-1} in June 2006 to 421.2 µg PNP g^{-1} soil h^{-1} in June 2007. Soil microbial biomass carbon (MBC) was correlated with both soil thermal conductivity (K) ($r = 0.4785$; $p < 0.05$), and K was also correlated with CO_2 ($r = -0.4577$; $p < 0.05$). These correlations would suggest an indirect influence of soil biological indices on greenhouse gas efflux.

Key words: Greenhouse gases, enzyme activity, beta-glucosidase, microbial biomass

INTRODUCTION

Increasing atmospheric concentration of greenhouse gases poses a serious treat to human health and the environment (Parry et al., 2007). Carbon dioxide, nitrous oxide and methane concentration in the atmosphere are increasing at annual rates of 0.5%, 0.75% and 0.75% respectively (Paul and Kimble, 1995). The United States accounts for approximately 25% of the global production of CO_2 with annual emission rates of H" 1.58 petagrams (pg) (Jackson and Schlesinger, 2004). Human activities such as those involved in agricultural practices impact various environmental processes (Zheng-chao and Zhou-ping, 2006; Mosier, 1998); and contribute to the global budget of greenhouse gases (Zheng-chao and Zhou-ping, 2006). The emission and/or consumption of greenhouse gases in general are affected by various soil biological, physical and chemical properties (Guo-yuan et al., 2006; Conrad, 1996; Ihessin et al., 2003), including soil organic matter content and management practices (Conrad, 1996; Adamsen and King, 1993; Nkongolo et al., 2006), and soil enzymes (Yuan et al., 2006). The relationships among soil physical and chemical properties and greenhouse gas effluxes have been documented (Agehara and Warncke, 2005; Jackson and Schlesinger, 2004; Fung et al., 2005; Paul and Kimble, 1995; Ginting et al., 2003; Avrahami et al., 2002). Adamsen and King (1993) investigated methane consumption in relation to temperature, vertical zonation, soil water content and nitrogen content. Additionally crop productivity and, by extension, soil organic matter content can be impacted by atmospheric

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CO_2 concentration (Heinemann et al., 2006).

The processes that maintain the balance of carbon and nitrogen between the atmosphere and soil are the carbon and nitrogen cycles, respectively (Keeling, 1997; Paul and Kimble, 1995); which are greatly influenced by soil microorganisms (Xuexia et al., 2006). However, greenhouse gas emissions from soils within a field vary immensely (Yanai et al., 2003) based on spatial variability of soil properties (Broos et al., 2007). Paro et. al. (2007), observed spatial and seasonal variation in greenhouse gas efflux across landscapes in a secondary forest. Johnson et al. (2007) also noticed similar spatial and seasonal variation in greenhouse gas efflux in a managed pasture. Lu et al. (2000) attributed seasonal patterns of methane (CH_4) emissions to variations in dissolved organic carbon (DOC), which they linked to differences in DOC released from plant roots (Jarecki and Lal, 2003; Uselman et. al., 2007; Froberg et. al., 2007). Ding et. al. (2007) described the interaction of soil temperature and soil moisture, and their combined influence on CO_2 emissions from soils in Henan, China. They found significant correlations between seasonal CO_2 fluxes and soil temperature and moisture. The indications from these studies are that greenhouse gas effluxes are influenced by both biotic and abiotic factors. However, a closer examination is needed to clearly understand relationships among soil microbial properties, management practices, and greenhouse gas efflux mechanisms. Our research objective was to investigate the relationship between spatial distribution of greenhouse gases, soil microorganisms, and microbial activity within a secondary forest in central Missouri.

MATERIALS AND METHODS

Research Site: The experiment was conducted in a permanent secondary forest on the Busby Farm at Lincoln University in Jefferson City, Missouri. The site has an area of 0.49 ha and is dominated by oak and hickory trees on a Gatewood-Moko silt loam (Oxyaquic Hapludalfs). Samples were collected from a total of 20 sampling locations arranged in complete random design.

CO_2, N_2O, and CH_4 measurements – Greenhouse gases, CO_2, N_2O, and CH_4 were measured as described in Paro et al. (2007). In brief, chambers were permanently installed to a depth of 0.03m. Air samples were collected with 50ml syringes, transferred to 200ml Tedlar bags (SKC Inc., Eighty Four, PA, USA). Samples were transported to the Dickinson Research Laboratory – Lincoln University, MO and analyzed for CO_2, N_2O, and CH_4 within two hours on a Shimadzu GC-14A Gas Chromatograph (Shimadzu Inc., Columbia, MD, USA)[1]. Fluxes were calculated using the equation: $F = \tilde{n} * V/A * \Delta C/\Delta t * (273/T) * \acute{a}$; where F is the gas production rate; $\tilde{n}$ is the gas density (kg m^{-3}) under standard conditions; V (m) and A (m) are the volume and area of the chamber; "C/"t is the ratio of change in the gas concentration in the chamber (10 m^{-3} m^{-3} h); T is the absolute temperature; and á is the transfer coefficient (12/44 for CO_2, 12/16 for CH_4, and 28/44 for NO_2) on a dry weight basis in units of µg *p*-nitrophenol (PNP) produced g^{-1} oven dry (o.d.) soil h^{-1}. *Soil treatments* – Soil samples were collected to a depth of 0 - 20 cm, sieved moist at <2mm and stored below 4^0C until time of analysis. Soils were pre-incubated at ambient temperature (~ 25 C) for 24 hours prior to analysis.

Soil chemical properties – Gravimetric soil water content for each sampling date at each sampling location was determined using the method describe by Zancan et al. (2006). Freshly sieved (<2mm) soils from each sample location was weighed in aluminum boats and dried at 105^0C until no further weight loss was observed. Results were used to convert relevant data from quantity/rate per gram of field moist soil to quantity/rate per gram of dry weight of soil. Total organic carbon (TOC) and total nitrogen (TN) were determined through combustion using a LECO

[1] Mention of trade name or commercial products is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA-ARS, Lincoln University, or the University of Missouri.

TruSpec carbon – nitrogen analyzer (LECO Corporation, St. Joseph, MI, USA).

Soil Biological Properties - Beta- glucosidase activity was assayed using a modified version of the method developed by Tabatabai (1994). Moist soil (1 g o.d.; <2mm) was placed in a 50ml flask to which 0.25ml of toluene, 4ml of pH 6.0 modified universal buffer (MUB), and 1ml of 0.5mol L^{-1} p-nitrophenyl-â-D-glucoside (PNG)solution were added. Samples were incubated at 37^0C for 1 hour. After incubation 1ml of 0.5mol L^{-1} $CaCl_2$ and 4ml of 0.1mol L^{-1}pH 12 tris(hydroxymethyl)aminomethane (THAM) buffer were added to stop the reaction. Suspensions were then filtered through Whatman # 2 filter paper under vacuum, and absorbance of the filtrates measured at 410 nm. â-glucosidase activities were measured in duplicate and reported on a dry weight basis in units of µg *p*-nitrophenol (PNP) produced g^{-1} oven dry (o.d.) soil h^{-1}.

Microbial biomass carbon (MBC) and nitrogen (MBN) were measured by chloroform fumigation extraction (CFE) modified from Anderson and Joergensen (1997). Soils were conditioned at 60% water holding capacity for 7 days prior to CFE. Five grams of soil was fumigated in a vacuum desiccator for 5 d, and then extracted by shaking in 0.5M K_2SO_4 for 1 hour. Non-fumigated soils were also extracted (0.5M K_2SO_4) at the time of fumigation. Extracts were filtered (Whatman glass fiber filter paper) and analyzed for TOC and TN using a Shimadzu total organic C and total N analyzer (Shimadzu Inc., Columbia, MD, USA). Microbial biomass C and N were calculated using a K_{ec} factor of 0.45 (Beck et al., 1997) and a K_{en} factor of 0.54 (Brooks et. al., 1985).

Statistical analysis – Statistical analysis of the data was performed using Statistix 8.1 for simple and summary statistics. Inverse Distance Weighting (ArcGIS 9.2) was used to produce interpolated maps; from experimental and model semi-variograms calculated with GS+ 5.1 software.

RESULTS AND DISCUSSIONS

Gas production rates ranged from 65.0 mg CO_2-C m^{-2} h^{-1} to 172.9 mg CO_2-C m^{-2} h^{-1} (mean 97.9 mg CO_2-C m^{-2} h^{-1}) for CO_2, 1.88 µg N_2O-N m^{-2} h^{-1} to 18.80 µg N_2O-N m^{-2} h^{-1} (mean 6.62 µg N_2O-N m^{-2} h^{-1}) for N_2O, and -158 µg CH_4-C m^{-2} h^{-1} to -12.5 µg CH_4-C m^{-2} h^{-1} (mean -71.5 µg CH_4-C m^{-2} h^{-1}) CH_4 in June 2006 (Table 1). In June 2007, production rates ranged from 74 mg CO_2-C m^{-2} h^{-1} to 143 mg CO_2-C m^{-2} h^{-1} (mean 94.5 mg CO_2-C m^{-2} h^{-1}) for CO_2, 10.5 µg N_2O-N m^{-2} h^{-1} to 45.48 µg N_2O-N m^{-2} h^{-1} (mean 24.61 µg N_2O-N m^{-2} h^{-1}) for N_2O, and -86.78 µg CH_4-C m^{-2} h^{-1} to 26 µg CH_4-C m^{-2} h^{-1} (mean -21.15 µg CH_4-C m^{-2} h^{-1}) for CH_4. The ranges of MBC and MBN were 72.8 mg C kg^{-1} soil to 277.17 mg C kg^{-1} soil (mean 139 mg C kg^{-1} soil), and 5.48 mg N kg^{-1} soil to 37.36 mg N kg^{-1} soil (mean 19.07 mg N kg^{-1} soil), respectively for June 2006 (Table 1). In June 2007 MBC and MBN ranged from 96.10 mg kg^{-1} soil to 276.48 mg kg^{-1} soil (mean 143.41 mg kg^{-1} soil) and 13.76 mg kg^{-1} soil to 38.5 mg kg^{-1} soil (mean 20.39 mg kg^{-1} soil) respectively (Table 1). There was therefore a slight but non-significant decrease in CO_2 efflux, and significantly higher efflux of N_2O and CH_4 in 2007 versus 2006. The higher efflux in N_2O and CH_4 may be related to similar changes in some soil thermal and biological properties from 2006 to 2007. For example â-glucosidase activity significantly increased from 228.5 µg PNP g^{-1} o.d soil in June 2006 to 421.2 µg PNP g^{-1} o.d. soil in June 2007. The average TOC in soil increased from 4.59% in June 2006 to 5.32% in June 2007. Similarly, the average TN increased from 0.29% to 0.33% in 2007 compared to 2006. Soil thermal properties also differed between 2006 and 2007; for example, diffusivity increased from 0.16 in 2006 to 0.46 in 2007.

Greenhouse gas efflux from our research site were highly variable, with coefficients of variation ranging from 28.41 to 61.31% in 2006 and ranging from 15.59 to 136.13% in 2007 (Table 1), which are similar to results of Rayment and Jarvis (1999) and Yanai et al. (2003). Paro et al. (2007) reported linear correlations among greenhouse gases and

soil thermal properties at this site. As indicated in their results the relationships tended to differ monthly. For example in June 2006, CO_2 was influenced by soil thermal diffusivity ($r = 0.4927$; $p < 0.05$), while in 2007 it was influenced by soil thermal conductivity ($r = -0.4577$; $p < 0.05$) and soil thermal resistivity ($r = 0.4540$; $p < 0.05$). Rayment and Jarvis (1999) attributed variation in greenhouse gas fluxes to spatial heterogeneity in micro-topography and the corresponding impact on soil moisture, and to the influences of atmospheric turbulence. Yanai et al. (2003) attributed spatial variability in N_2O fluxes to variations in organic matter content and soil moisture. Therefore they inferred that denitrification may have been the driving force behind N_2O fluxes. For our research soil moisture was also found to influence CH_4 emissions ($r = 0.4551$; $p < 0.05$) (Table 3). However, other gases, specifically CO_2 and N_2O, were not significantly correlated with soil moisture (Tables 2 & 3). However, trends from isarithmic maps were similar for greenhouse gases and some soil properties in 2006 (Figures 1 & 2) and 2007 (Figures 3 & 4). For example, in both 2006 (Figures 1 & 2) and 2007 (Figures 3 & 4) greenhouse gas emissions and soil moisture, MBC, MBN, and â-glucosidase activity all tended to be higher in the northern section of the field, and decreased towards the southern section of the field. These trends may reflect influences of micro-topography (Rayment and Jarvis, 1999) as the field in this study had a higher elevation in the northern section compared to the southern section.

In addition there were significant correlations among soil biological properties and soil thermal properties. Soil MBC was significantly correlated with soil thermal conductivity ($r = -0.4617$; $p < 0.05$) and soil thermal resistivity ($r = 0.5703$; $p < 0.05$) for June 2006. Similarly for that sampling period CO_2 fluxes were significantly correlated with soil thermal diffusivity ($r = 0.4927$). â-glucosidase activity in 2006 also correlated significantly with soil thermal conductivity ($r = -0.5724$; $p < 0.05$) and soil thermal resistivity ($r = 0.6248$; $p < 0.05$). Other soil properties correlating with soil thermal properties in 2006 were TOC and TN (data not shown). Correlations among soil thermal properties and greenhouse gases and among soil thermal properties and soil biological properties were also observed the following year (June 2007); for example soil thermal conductivity was correlated with both MBC ($r = 0.4785$; $p < 0.05$) and CO_2 ($r = -0.4577$; $p < 0.05$). The relationship between soil thermal properties and greenhouse gas fluxes and the corresponding correlations between soil thermal properties and soil biological factors (MBC, enzyme activity) would suggest an indirect influence of soil biological indices on greenhouse gas efflux. Norris et al. (2002) observed differences in soil microbial community profiles along a thermal gradient; Tanaka and Hashimoto (2006) also observed relationships among soil thermal properties, soil respiration, and CO_2 fluxes. Xuexia et al. (2006) found a positive correlation between â-glucosidase activity and CO_2 efflux.

Table 1. Descriptive statistics for gas fluxes CO_2, N_2O, and CH_4, and soil biological and thermal properties.

	Minimum	Mean	Maximum	CV %
June 2006				
CO_2 mg CO_2-C m^{-2} h^{-1}	**65.03**	**97.92**	**172.90**	**28.11**
N_2O µg N_2O-N m^{-2} h^{-1}	**1.88**	**6.62**	**18.80**	**61.31**
CH_4 µg CH_4-C m^{-2} h^{-1}	**-157.99**	**-71.46**	**-12.54**	**53.83**
TOC g kg^{-1} soil	**35.30**	**45.90**	**81.5**	**27.35**
TN g kg^{-1} soil	**2.00**	**2.90**	**5.3**	**25.77**
MBC mg kg^{-1} soil	**72.80**	**139.02**	**277.17**	**33.21**
MBN mg kg^{-1} soil	**5.48**	**19.07**	**37.36**	**38.91**
Soil moisture (%)	**24.69**	**31.44**	**38.75**	**13.37**
β-glucosidase	**140.04**	**228.54**	**355.66**	**23.52**
T (^{0}C)	**18.00**	**18.48**	**19.00**	**1.40**
K ($wm^{-1}c^{-1}$)	**0.29**	**0.60**	**0.96**	**37.03**
D ($mm^{-2}s^{-1}$)	**0.10**	**0.16**	**0.23**	**23.92**
R (m^0cw^{-1})	**1.04**	**1.90**	**3.42**	**36.60**
June 2007				
CO_2 mg CO_2-C m^{-2} h^{-1}	**74.09**	**94.51**	**142.96**	**15.59**
N_2O µg N_2O-N m^{-2} h^{-1}	**10.51**	**24.61**	**45.58**	**38.70**
CH_4 µg CH_4-C m^{-2} h^{-1}	**-86.78**	**-21.15**	**26.02**	**136.13**
TOC g kg^{-1} soil	**33.8**	**53.2**	**77.8**	**21.99**
TN g kg^{-1} soil	**2.0**	**3.3**	**5.4**	**26.55**
MBC mg kg^{-1} soil	**96.10**	**143.41**	**276.48**	**29.54**
MBN mg kg^{-1} soil	**13.76**	**20.39**	**38.50**	**30.21**
Soil moisture (%)	**19.22**	**30.31**	**43.61**	**15.50**
β-glucosidase µg PNP g^{-1} soil	**209.10**	**421.16**	**679.58**	**27.60**
T (^{0}C)	**21.20**	**21.89**	**22.40**	**1.63**
K ($wm^{-1}c^{-1}$)	**0.42**	**0.77**	**1.33**	**31.08**
D ($mm^{-2}s^{-1}$)	**0.30**	**0.46**	**0.86**	**32.18**
R (m^0cw^{-1})	**0.75**	**1.42**	**2.30**	**31.32**

Total organic carbon (TOC), total nitrogen (TN), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), â-glucosidase activity (â-glucosidase), soil temperature (T), soil thermal conductivity (K), soil thermal diffusivity (D), and soil thermal resistivity (R).

Table 2. Correlation matrix for greenhouse gases and soil biological properties for June 2006.

	TOC	TN	MBC	MBN	GLU	GM	CO2	N_2O	CH_4
TOC	1								
TN	0.9391***	1							
MBC	0.7835***	0.8399***	1						
MBN	0.5283*	0.5729*	0.8214***	1					
GLU	0.6418*	0.7203***	0.6855*	0.4447	1				
GM	0.4694*	0.4422	0.2508	0.0581	0.2962	1			
CO2	-0.2035	-0.163	-0.3589	-0.2114	-0.1552	0.1078	1		
N2O	-0.0335	0.0448	0.0426	0.0297	0.0565	0.3596	0.2504	1	
CH4	0.1093	0.0865	0.0707	0.0551	0.0551	0.2878	-0.1046	0.4458	1

***, * significantly different at 0.001 and 0.05 probability level

Total organic carbon (TOC), total nitrogen (TN), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), â-glucosidase activity (GLU), gravimetric soil water content (GM), carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4).

Table 3. Correlation matrix for greenhouse gases and soil biological properties for June 2007.

	TOC	TN	MBC	MBN	GLU	GM	CO_2	N_2O	CH_4
TOC	1								
TN	0.7991***	1							
MBC	0.7402***	0.8573***	1						
MBN	0.6160*	0.7276***	0.9431***	1					
GLU	0.7910***	0.8273***	0.8170***	0.6527*	1				
GM	0.4939	0.4302	0.3695	0.2403	0.6319*	1			
CO_2	0.1087	0.1041	0.2301	0.3302	-0.0153	-0.0153	1		
N_2O	-0.157	-0.0628	-0.1835	-0.2033	-0.1219	0.1677	0.0189	1	
CH_4	0.2703	0.1965	0.2996	0.2553	0.2838	0.4551*	0.1438	0.3184	1

***, * significantly different at 0.001 and 0.05 probability level

Total organic carbon (TOC), total nitrogen (TN), microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), â-glucosidase activity (GLU), gravimetric soil water content (GM), carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4).

Figure 1. Spatial distribution of greenhouse gases for June 2006.

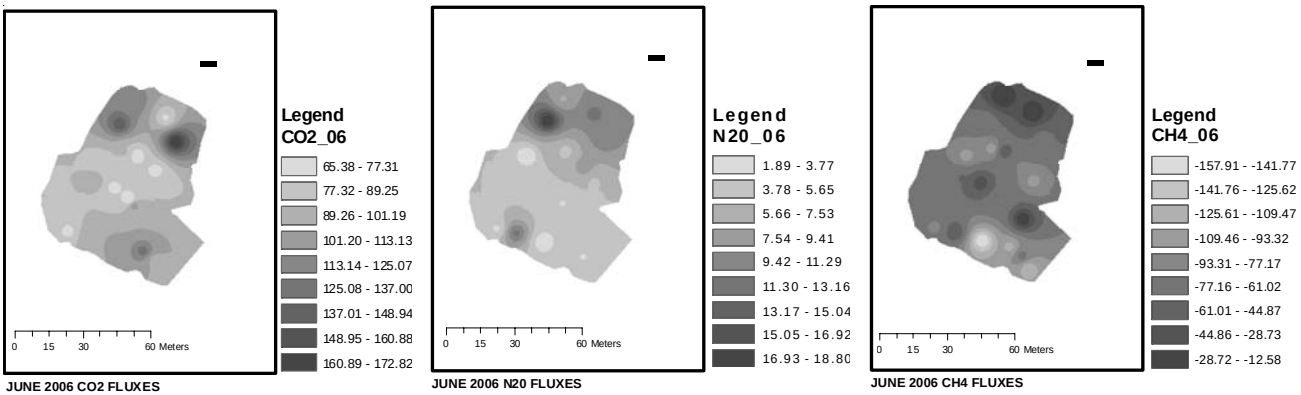
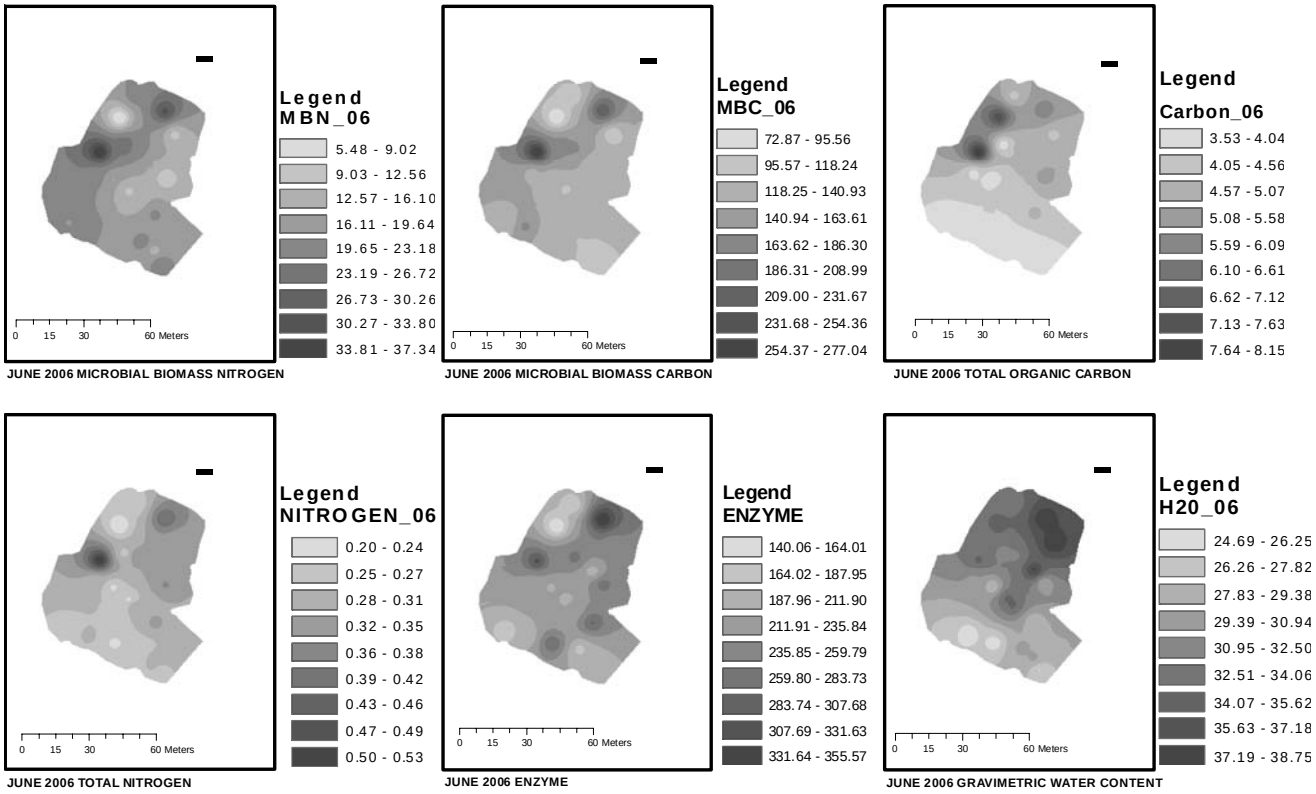
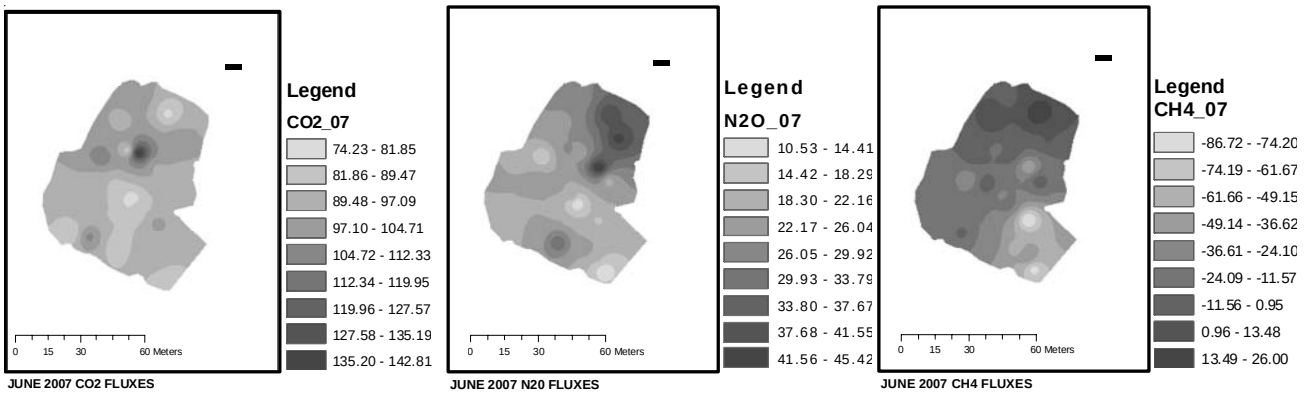


Figure 2. Spatial distribution of soil biological properties for June 2006.



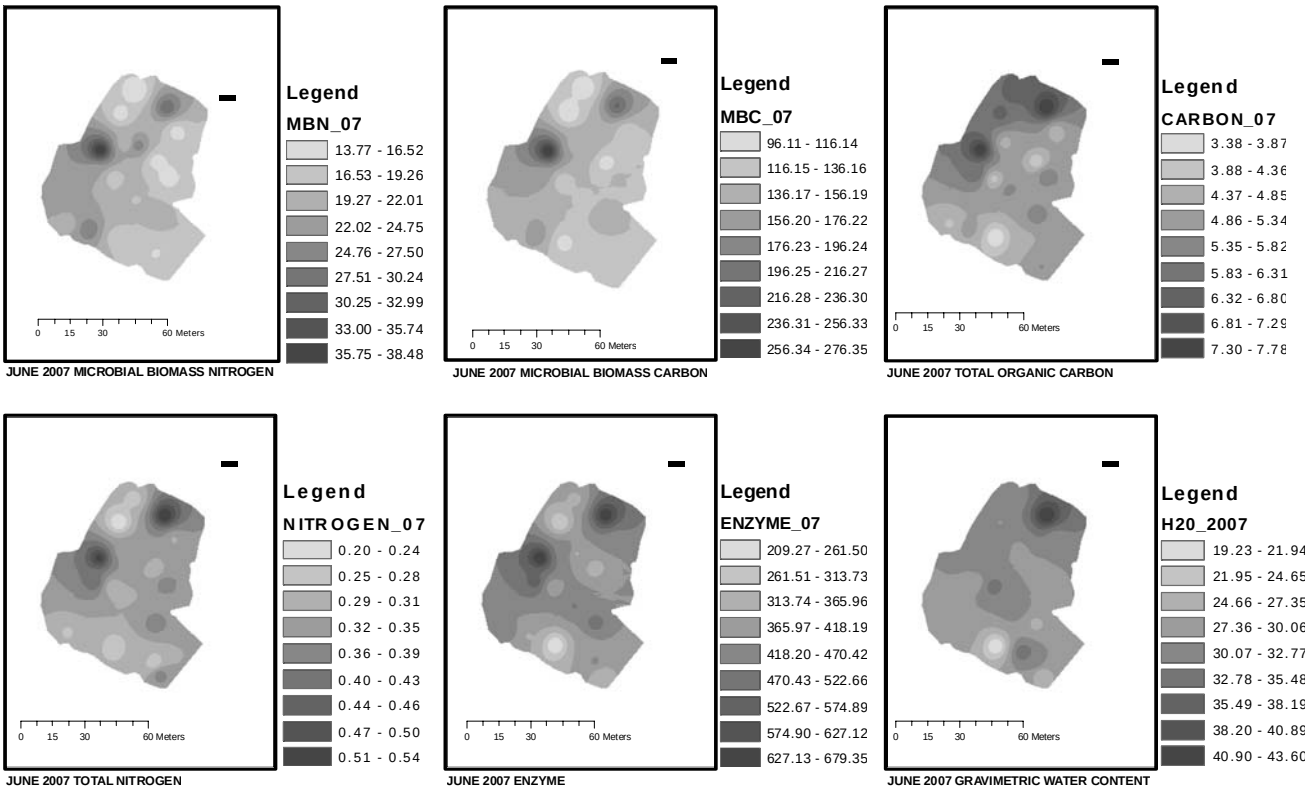
Microbial biomass nitrogen (MBN), microbial biomass carbon (MBC), total organic carbon (TOC), total nitrogen (TN), â-glucosidase (enzyme), and gravimetric water content [See Table 1 for individual map units].

Figure 3. Spatial distribution of greenhouse gases June 2007.



Carbon dioxide (CO_2), nitrous oxide (N_2O), methane (CH_4) [See Table 1for individual map units].

Figure 4. Spatial distribution of soil biological properties for June 2007.



Microbial biomass nitrogen (MBN), microbial biomass carbon (MBC), total organic carbon (TOC), total nitrogen (TN), â-glucosidase (enzyme), and gravimetric water content [See Table 1 for individual map units].

Although, we did not find any direct correlations among greenhouse gases and soil biological properties; the results suggest that greenhouse gas fluxes may be indirectly related to soil biological properties. It is common knowledge that soil properties such as moisture, soil type, temperature, etc. can have a masking effect on soil biological properties (Jensen et al., 1997). Therefore further research is needed to clarify the relationships among soil biological properties (MBC, MBN, enzymatic activity, etc.), and greenhouse gas fluxes. Khorsandi and Nourbakhsh (2008) have suggested incubation studies at constant temperature and moisture as probable methods of reducing the compounding influences of moisture and temperature on relationships of soil biological properties with gas efflux.

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