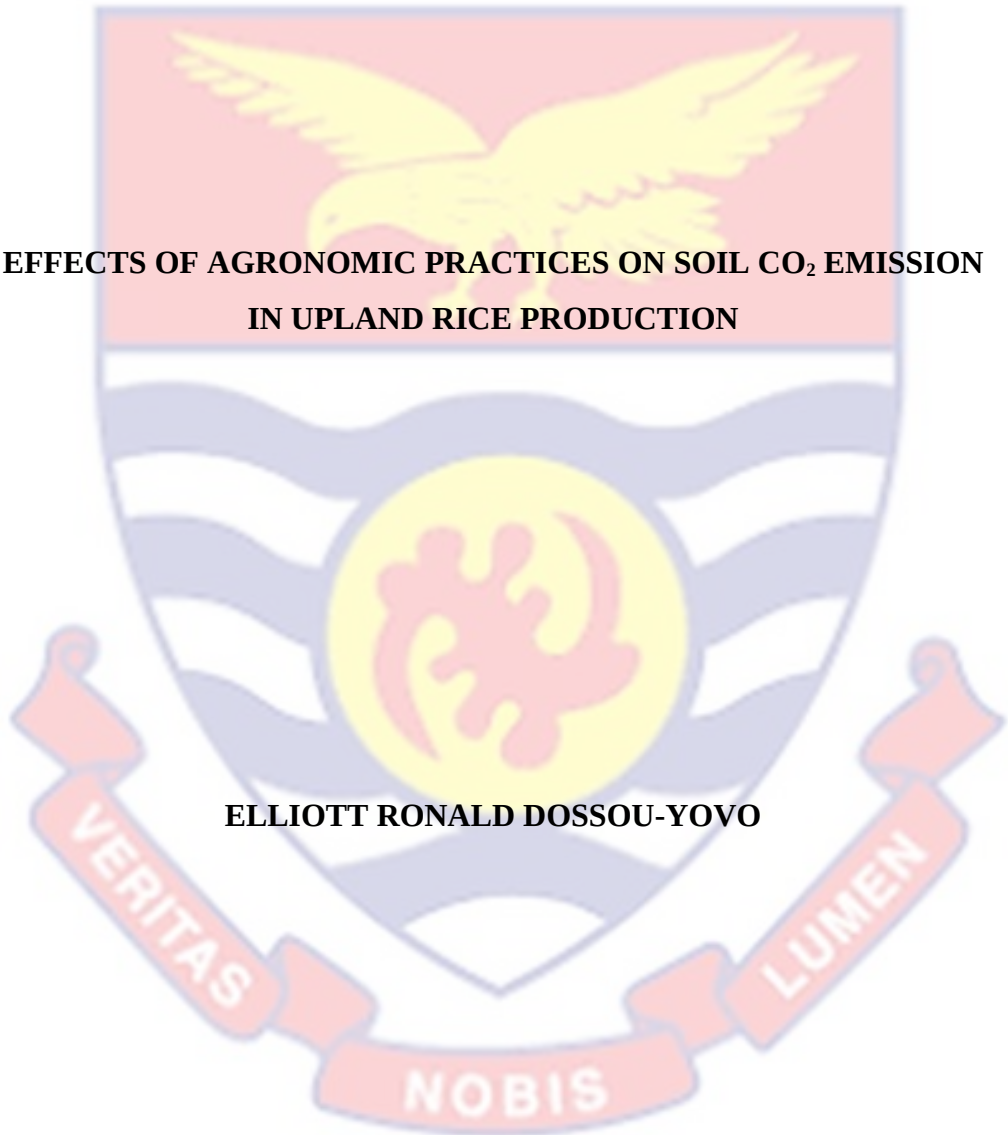


UNIVERSITY OF CAPE COAST

**EFFECTS OF AGRONOMIC PRACTICES ON SOIL CO₂ EMISSION
IN UPLAND RICE PRODUCTION**

ELLIOTT RONALD DOSSOU-YOVO



2016



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University of Cape Coast

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**EFFECTS OF AGRONOMIC PRACTICES ON SOIL CO₂ EMISSION
IN UPLAND RICE PRODUCTION**

BY

ELLIOTT RONALD DOSSOU-YOVO

Thesis submitted to the Department of Soil Science of the School of
Agriculture, College of Agriculture and Natural Sciences, University of Cape
Coast, in partial fulfillment of the requirements for the award of Doctor of
Philosophy degree in Land Use and Environmental Science

MARCH 2016

DECLARATION

Candidate's Declaration

I hereby declare that this thesis is the result of my own original research and that no part of it has been presented for another degree in this university or elsewhere.

Candidate's Signature:  Date: 02/03/2016

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Supervisors' Declaration

We hereby declare that the preparation and presentation of the thesis were supervised in accordance with the guidelines on supervision of thesis laid down by the University of Cape Coast.

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ABSTRACT

To explore effective ways to decrease soil CO₂ emission and increase soil carbon storage and grain yield, field experiments were conducted on two upland rice soils (Lixisol and Gleyic Luvisol) in northern Benin. The treatments comprised two tillage systems (no-tillage, and manual tillage), two rice straw managements (no rice straw, and rice straw mulch at 3 Mg ha⁻¹) and three nitrogen fertilizer levels (no nitrogen, 60 kg ha⁻¹, and 120 kg ha⁻¹). Soil CO₂ emissions were higher in tilled treatments than in no-tilled treatments, and higher in fertilized treatments compared with non-fertilized treatments. Under the current management practices (manual tillage, with no residue and no nitrogen fertilization) in upland rice fields in northern Benin, the carbon added as aboveground and root biomass was not enough to compensate for the loss of carbon from organic matter decomposition, rendering the upland rice fields as net sources of atmospheric CO₂. With no-tillage, 3 Mg ha⁻¹ of rice straw mulch and 60 kg N ha⁻¹, the soil carbon budget was zero on the Lixisol and 0.6 Mg C ha⁻¹ on the Gleyic Luvisol. The highest response of rice yield to nitrogen fertilizer addition was obtained for 60 kg N ha⁻¹ with 3 Mg ha⁻¹ of rice straw mulch for the two tillage systems. Soil CO₂ emission per unit grain yield was lower under no-tillage, rice straw mulch and nitrogen fertilizer treatments. No-tillage combined with application of 3 Mg ha⁻¹ of rice straw mulch and 60 kg N ha⁻¹ reduced soil CO₂ emission, increased soil carbon budget and upland rice yield in northern Benin.

KEY WORDS

Heterotrophic respiration

Management practices

Root respiration

Soil CO₂ emission

Upland rice

Yield



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DEDICATION

To my parents,

Julien and Flore Dossou-Yovo



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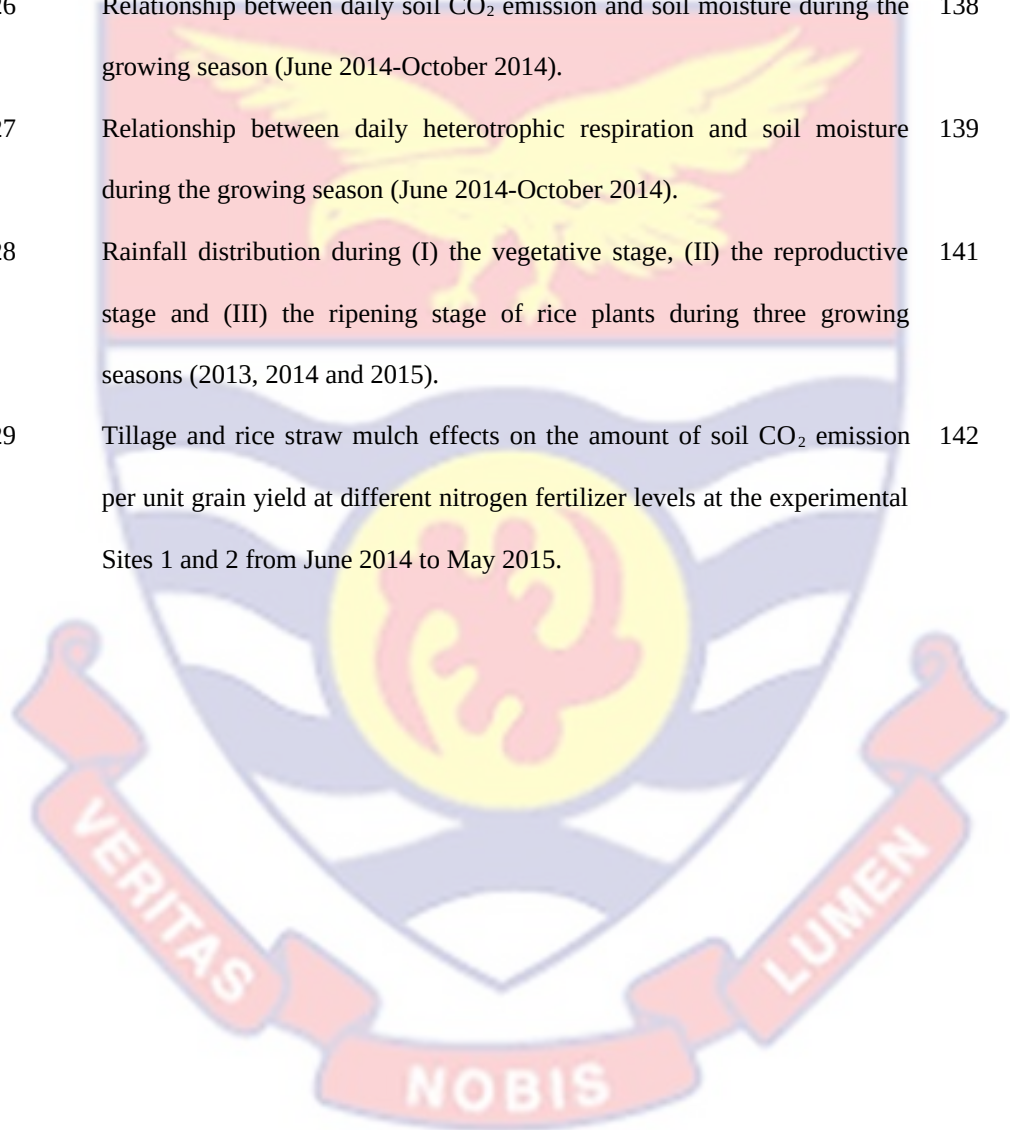
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LIST OF ACRONYMS

C	Carbon
CH ₄	Methane
CO ₂	Carbon dioxide
DAS	Days After Sowing
DOY	Day Of the Year
FAO	Food and Agriculture Organization
GRP	Graduate Research Programme
IPCC	Intergovernmental Panel on Climate Change
Mg C	Megagram of Carbon (1 Mg C = 10 ⁶ g C)
N	Nitrogen
N ₂ O	Nitrous oxide
Pg C	Petagram of Carbon (1 Pg C = 10 ¹⁵ g C)
PVC	Polyvinyl Chloride
R _h	Heterotrophic (microbial) respiration
R _r	Root respiration
SOC	Soil Organic Carbon
θ _v	Volumetric soil water content
WASCAL	West Africa Science Service Center on Climate Change and Adapted Land Use
UCC	University of Cape Coast

CHAPTER ONE: INTRODUCTION

Soil organic matter (SOM) plays a crucial role in maintaining soil health and its productivity potential (Baker, Ochsner, Venterea, & Griffis, 2007). However, most of the world's agricultural soils have become depleted in organic matter over the years. This is because the dominant form of agriculture is based on tillage, which accelerates the decomposition of SOM (Gangwar, Singh, Sharma, & Tomar, 2006). At the same time, there has been a tendency for tillage agriculture to remove much of the crop residues, thus leaving the soil starved of substrate for soil organisms to maintain soil structure. Such agricultural soils are not able to offer the best factor productivities for production inputs such as nutrient and water, and are not able to provide environmental services such as carbon sequestration (Corsi, Friedrich, Kassam, Pisante, & Sa, 2012). In addition to sustainable production intensification, there is a need to transform farming practices to sequester carbon so that climate change mitigation becomes an inherent property of future farming systems. However, there appears to be a certain degree of uncertainty about the role of agriculture in carbon sequestration and in reducing greenhouse gas emissions in many regions of West Africa where there is insufficient data to make realistic estimates. This study evaluates the effects of agronomic practices on soil CO₂ emission, soil carbon budget and crop yield with the aim to provide an understanding of the benefits associated with alternative tillage and fertilization practices.

Background to the Study

Climate change caused mainly by increased concentrations of CO₂ in the atmosphere (IPCC, 2013), and food security problems owing to the fast-growing human population and loss of farmland have become global issues that seriously threaten developing countries (Liu, Liu, Bian, Ma, & Lang, 2014). Agriculture is an important source of CO₂ emissions, and its contribution to climate change is approximately 14% on an annual basis (Vermeulen, Campbell, & Ingram, 2012). Small changes in the magnitude of soil CO₂ emission could have a large effect on the concentration of CO₂ in the atmosphere (Schlesinger & Andrews, 2000). In order to reduce and mitigate the potential negative effects of climate change on ecosystems and human well-being, a series of strategies are needed to reduce CO₂ emissions and atmospheric CO₂ concentration (Vermeulen et al.). In this respect, enhancement of soil carbon sequestration in agricultural systems is one of the strategies to both offset atmospheric CO₂ increases and achieve food security (Lal, 2004; Lal, Negassa, & Lorenz, 2015).

Precise measurement and verification of the amount of carbon sequestered in the soil have proven to be difficult. The use of soil organic carbon (SOC) of depleted land as a sink for some of the excess CO₂ appears to be a practical and cost effective method for reducing atmospheric CO₂ levels (Post & Kwon, 2000). The basic thought behind reducing emissions through SOC sequestration by changes in land use relies on the restoration of original native carbon levels. The magnitude of SOC storage depends on a range of

factors such as soil type, land use, annual input of C, plant type, and the severity of degradation (Johnson, Franzluebbers, Weyers, & Reicosky, 2007).

Rice has become the most rapidly growing food source in West Africa as a consequence of population growth and a shift in consumer preferences for rice, especially in urban areas (Balasubramanian, Sie, Hijmans, & Otsuka, 2007). The two main ecosystems of rice in West Africa are upland and lowland rice. Upland rice, known as aerobic rice, is generally grown in non-flooded, well drained soils on level to steeply sloping fields. Lowland rice, known as paddy rice, is generally grown on soils that are flooded or irrigated (Andriessse & Fresco, 1991). The carbon dynamics in upland rice fields significantly differs from that in lowland rice fields. In upland rice fields, the carbon accumulated in the soil is constantly released to the atmosphere due to aerobic decomposition (Nakadai, Koizumi, Bekku, & Totsuka, 1996). In lowland rice fields, during the submerged period of rice cultivation, CO₂ emission from the soil is limited due to a decrease in the microbial respiration in the soil deoxidized under the flooding water and also carbon fixation by algal photosynthesis. During the submerged period in lowland fields, on the contrary, methane emission from the soil increases (Epule, Peng, & Mafany, 2011). In a comparative analysis of the soil carbon budgets of upland and paddy rice fields, Nishimura et al. (2008) found a carbon accumulation in the soil of the paddy rice field from +79 to +137 g C m⁻² y⁻¹, and a significant carbon loss in the upland rice field from -343 to -275 g C m⁻² y⁻¹. As paddy rice field may be a well-carbon balanced agricultural system, often resulting in a positive increase in carbon, effective management practices are needed in

upland rice agro-ecosystems to reduce soil carbon emission in order to maintain soil carbon balance and soil fertility (Nishimura et al.).

Statement of the Problem

In Benin, rainfed upland rice ecosystems account for about 27% of the total rice area (Diagne, Amovin-assagba, Futakuchi, & Wopereis, 2013). Rice is typically grown under intensive tillage in slash-and-burn systems and farmers rely on extended fallows to restore soil fertility. However, rapid population growth and increased demand for land have led to shortened fallow periods, which in turn have resulted in declining soil organic carbon and rice yield (Saito, Azoma, & Oikeh, 2010).

Application of plant residues as mulch, instead of burning, has beneficial effects for replenishing soil organic carbon (Al-Kaisi & Yin, 2005), and the return to the soil of 1 Mg ha⁻¹ of straw (rice, wheat or maize) each year can sequester about 0.13 Mg C ha⁻¹ yr⁻¹ (Lu, Wang, Han, & Ouyang, 2009). However, the effects of straw mulching on soil CO₂ emission and crop yield have not been conclusively agreed upon among reported studies. Decomposition of straw added to soil and subsequent release of CO₂ and nutrients are governed by many factors such as soil moisture, soil temperature and soil nitrogen content (Abro, Tian, You, & Wang, 2011). Soil CO₂ emission was reported to be higher in straw-mulched than in non-mulched rice fields (Bhattacharyya, Roy, & Neogi, 2012). In contrast, cumulative soil CO₂ emission was 24% lower for no-tillage systems with residue amendment than without in corn-soybean fields (Al-Kaisi & Yin, 2005). In the north China

Plain, soil CO₂ emissions in a maize field were 35.4% and 19.9% lower in mulched treatments than in non-mulched treatments in 2012 and 2013, respectively (Liu et al., 2014). Straw mulch with optimum N fertilizer in zero tillage reduced soil CO₂ emissions and gave better yields (Tanveer, Wen, Lu, Zhang, & Liao, 2013). However, the reports on the effect of straw mulching on soil CO₂ emission and crop yield are not consistent; therefore, further study is required to assess the effect of mulching on soil carbon emission and utilization in cropland.

Tillage is an integral part of rice cultivation in Benin. This technique, however, is considered as one of the most important sources of CO₂ emissions to the atmosphere. Studies have shown that 30-50% of soil carbon has been lost through intensive tillage practices (Baker et al., 2007), and major carbon losses from soils in the form of CO₂ occur immediately after tillage (Al-Kaisi & Yin, 2005; La Scala, Bolonhezi, & Pereira, 2006). While it has been well documented that no-tillage, compared with intensive tillage, reduced soil CO₂ emission, its effect on crop yields has not been conclusively agreed upon among reported studies. Tsuji, Yamamoto, Matsuo, and Usuki (2000) reported that upland rice yield was higher in no-tillage management than in conventional tillage management in two out of three years in Japan. However, Saito et al. (2010) found that conversion to zero tillage may decrease upland rice yield in southern Benin. The reasons for such contrasting results are not clear; but they might be due to differences in agro-ecosystems and fertilization practices.

Soil nitrogen availability is a major constraint to upland rice productivity in Benin (Saito et al., 2010). Several studies reported the use of low amounts of nitrogen fertilizers by rice farmers which resulted in lower yields (Fageria, de Morais, & dos Santos, 2010). However, there is considerable discussion about the effects of nitrogen fertilization on soil CO₂ emission and soil carbon sequestration. Some studies have shown a suppressive effect (Al-Kaisi, Kruse, & Sawyer, 2008) and other a positive stimulatory effect (Mulvaney, Khan, & Ellsworth, 2009) of nitrogen fertilization on soil CO₂ emission. It has been also suggested that increases in nitrogen fertilization levels may promote soil carbon sequestration, due to increases in aboveground biomass and especially root biomass, which can contribute to more stable SOC than aboveground residues (Rasse, Rumpel, & Dignac, 2005). However, potential increases in carbon input from increases in nitrogen fertilization level could be counter balanced by increases in carbon mineralization and CO₂ emissions (Zhou et al., 2014). Also here further research is needed to examine the effects of nitrogen fertilization on soil CO₂ emission and soil carbon sequestration.

Currently, there are few studies that have evaluated the effects of farming management practices on soil CO₂ emission, soil carbon budget and crop yields for a suggestion of alternative farming strategies to the smallholder farmers (Wilhelm, 2004; Dolan, Clapp, Allmaras, Baker, & Molina, 2006). Additionally, sustainability of farming strategies will also depend predominantly on the cropping system, climate and soil type (Mu, Kimura, Toma, & Hatano, 2008) which needs to be specified regionally. In this

context, it is necessary to study the effects of tillage systems, rice straw mulch and nitrogen application on soil CO₂ emission, soil carbon budget and upland rice yield in Benin.

Purpose of the Study

The purpose of the study is to identify agronomic practices that will reduce soil CO₂ emission and increase soil carbon budget and upland rice yield in northern Benin.

Research Objectives and Questions

Research Objectives

The objectives of the study are to:

- examine the effects of tillage systems, rice straw mulch and inorganic nitrogen fertilizer application on soil CO₂ emission,
- examine the effects of tillage systems, rice straw mulch and inorganic nitrogen fertilizer application on soil carbon budget,
- determine the factors controlling soil CO₂ emission, and
- identify an appropriate combination of tillage systems, rice straw mulch and inorganic nitrogen fertilization to reduce soil CO₂ emission and increase soil carbon budget and upland rice yield in northern Benin.

Research Questions

I hypothesized that potential losses in soil organic carbon and crop yield in general due to tillage and rice straw removal/burning in upland rice fields in northern Benin could be reduced by using agronomic practices that have lower intensity of tillage, rice straw as a soil mulch material and high inorganic nitrogen fertilizer application rates.

To be able to test this hypothesis, the research questions are described below.

- What are the effects of no-tillage with rice straw mulch under different levels of inorganic nitrogen fertilizer application on soil CO₂ emission in upland rice fields?
- What are the effects of no-tillage with rice straw mulch under different levels of inorganic nitrogen fertilizer application on soil carbon budget in upland rice fields?
- Which factors control soil CO₂ emission in upland rice fields?
- How can tillage systems, rice straw mulch and inorganic nitrogen fertilizer be optimized to increase upland rice yield in northern Benin?

Significance of the Study

Emissions from agricultural production systems are important in the greenhouse gas budgets of West Africa (Bond-Lamberty & Thomson, 2010). Gaps and uncertainties in knowledge – of emission rates, mitigation opportunities, incentives to change practices, and institutions that enable adoption – slow down the transition towards low emissions agricultural

development (Epule, 2015). The results from this study published in *Soil & Tillage Research* and in *International Journal of Agronomy and Agricultural Research* provide a comprehensive assessment of the effects of agronomic practices on soil CO₂ emission, soil carbon budget and upland rice yield. The results can be used to assist national policy makers, investors and other decision-makers who seek to understand the mitigation potential of agronomic practices and prioritize mitigation actions. The United Nations Framework Convention on Climate Change (UNFCCC) experts and reviewers will benefit from the datasets produced, including documented methods and limitations, which can be used in the national greenhouse inventories mandated by the UNFCCC. Finally, the results will be beneficial to the farmers who seek to reduce the loss of carbon in the form of CO₂ from their fields in order to increase the stock of soil organic carbon and the crop yield.

Delimitations

The study was conducted in the Tetonga catchment in the district of Materi in northern Benin. The catchment is located between 1°01' E and 1°14' E and 10°42' N and 10°57' N and belongs to the Sudanian Savannah agro-ecological zone of West Africa. The study was conducted on upland rice soils and examined the effects of tillage, straw mulch and nitrogen fertilizer application on soil CO₂ emission, soil carbon budget and rice yield. The study was not conducted in lowlands. Other greenhouse gases such as methane and nitrous oxide were not quantified in the study.

Limitations

The soil CO₂ measurements were conducted by placing the gas-tight soil respiration chambers on two collars that were placed in the center of each plot. Measurements of soil CO₂ with three collars placed in the center of each experimental plot instead of two collars may capture more accurately the spatial variability of soil CO₂ emission in each experimental plot.

Definition of Terms

Soil CO₂ emission or soil respiration

Soil CO₂ emission or soil respiration is defined as the production of carbon dioxide by organisms and the plant parts in soil. These organisms are soil microbes and fauna, and the plant parts are roots and rhizomes in the soil (Luo & Zhou, 2010). Although the definition of soil usually does not include dead plant materials at the soil surface that have not been well decomposed, CO₂ production via litter decomposition in the litter layers is generally included in soil CO₂ emission (or soil respiration) in many publications and, for the sake of simplicity, in this study as well.

Root respiration or autotrophic respiration

Root respiration or autotrophic respiration is defined as the respiration of the living root tissue. Plants respire some of the carbon compounds which were generated by photosynthesis. When this respiration occurs in roots, it adds to soil respiration (Luo & Zhou, 2010).

Microbial respiration or heterotrophic respiration

Microbial respiration or heterotrophic respiration is a measure of the carbon dioxide released from the soil by microbes decomposing soil organic matter (Luo & Zhou, 2010).

Soil carbon budget

Soil carbon budget is defined as the difference between gains of biomass carbon or input and losses of biomass carbon or output. Input of biomass carbon is composed of aboveground carbon input, root carbon input including root exudates, deposition by water run-on or wind-blown sediments and management-related input of biomass carbon including compost, cover crops, crop/animal residues, among others. Output of biomass carbon is composed of oxidation/ mineralization of soil organic carbon, erosion and leaching (Lal et al., 2015).

No-tillage

No-tillage is defined as a system of farming that consists of planting without tillage and with the use of herbicides to suppress weeds (Baker et al., 2007).

Tillage

Tillage in this study refers to the use of hoe to plough the soil to the depth of 15-20 cm before planting.

Organisation of the Study

This thesis is organized into six chapters. The first chapter presents the background to the study, the statement of the problem, the objectives, the research questions, and the significance of the study, the delimitations, the limitations and the definition of terms. The second chapter presents the literature review focusing on soil respiration and carbon sequestration in agricultural soils. The third chapter briefly presents the climate and the soil properties of the study area. This chapter also presents the materials and methods used for study design, data collection and data analysis. The fourth chapter presents the results for each specific objective. The fifth chapter presents the discussion of the results. The sixth chapter presents the summary of the research findings, the conclusions and the recommendations.

Chapter Summary

Chapter one presents the problem of decreasing soil organic carbon with years of cultivation faced by many farmers over the world. It describes the causes of the loss of SOC and how this loss enhanced the concentration of CO₂ in the atmosphere. Chapter one points out the existing knowledge gaps, controversies to be resolved and what previous researches have not been able to resolve. Chapter one also presents the purpose of the study; the research objectives, questions and significance. Finally, chapter one presents the delimitations, limitations, the definitions of terms as used within the context of the study and the organization of the thesis.

CHAPTER TWO: LITERATURE REVIEW

The study examined the effects of agronomic practices on soil CO₂ emission, soil carbon budget and upland rice yield. Chapter two presents the importance of rice in Benin, the rice growing environments in Benin, the soil carbon stock and its regulation, the effects of soil carbon stock on crop yields, the processes of CO₂ production in soil and transport from soil to the atmosphere, the methods of measurements and estimations of soil CO₂ emission and the carbon sequestration potentials in agricultural soils.

Importance of rice in Benin

Rice is the most rapidly growing food commodity in Benin, mainly driven by urbanization. The opportunity costs of women's labour and the ease and rapidity of cooking rice are key factors in urban settings. Urbanization is often accompanied by increased consumption of food away from the home, which has spurred rice demand due to the convenience of rice storage, preparation and cooking. With the proportion of Africans living in urban areas expected to increase from the current 38% to 48% by 2030, rice consumption in Africa is expected to continue to grow for the foreseeable future. Household surveys reveal that urban consumers on lower incomes tend to spend a greater share of their total budget on rice than higher-income households (AfricaRice, 2011).

In Benin, the rice production is far below the rice demand (Seck, Touré, Coulibaly, Diagne, & Wopereis, 2013). The rice self-sufficiency rate

was about 26% in 2014, resulting in the need for annual imports to meet the growing rice demand (Index-Mundi, 2015). Given the large amount of rice that Benin currently buys on the international market (e.g., 350,000 metric tons were imported in 2014) (Figure 1); an increase in local rice production is of great importance for increasing food security.

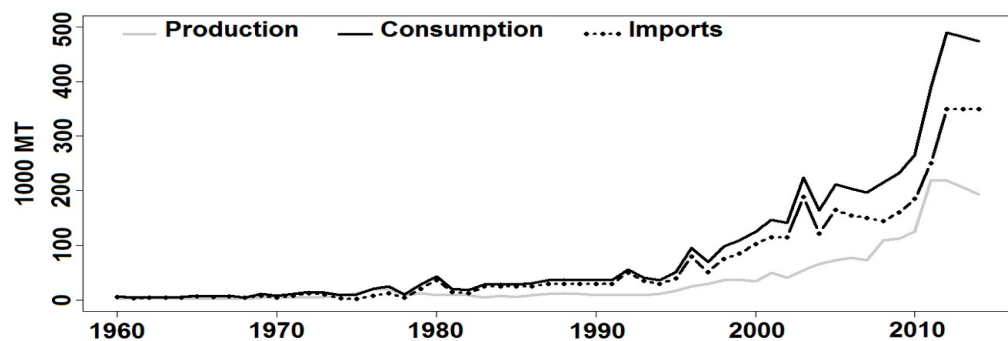


Figure 1: Milled rice production, consumption and imports from 1960 to 2014 in Benin.

Source: Index-Mundi (2015)

Rice-growing environments in Benin

Rice is an extremely versatile crop which can grow under a range of water regimes (in dry-and wetland conditions) and temperatures (at low and high altitudes and latitudes) (Saito et al., 2013). The various rice environments are characterized mainly by the main source of water for the plant -for example, rainfall (direct rainfall and/ or inflow), irrigation (water controlled through a system of canals, etc.), water table, uncontrolled flood water, and sea/brackish water. This has led, in general, to the distinguishing of rainfed

upland, rainfed lowland, irrigated upland, irrigated lowland, mangrove-swamp and deep-water environments.

Figure 2 depicts in a schematic manner the three major rice-growing environments in Benin: upland, rainfed lowland and irrigated lowland (WARDA, 2004). Upland environments are situated at the high end of the toposequence, where rice depends solely on rainfall as the water table is out of the reach of rice roots for much of the growing season. At the lower end of the toposequence, rice plants can reach the water table or profit directly from flood water. Along the toposequence, interactions exist between environments (e.g. water and nutrient flow from upland to lowland).

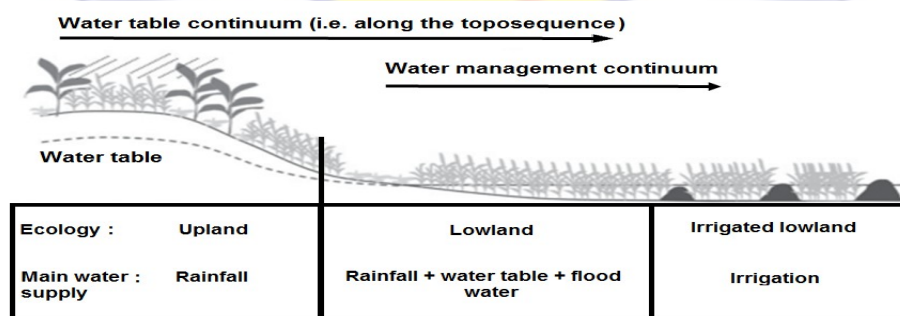


Figure 2: Major rice growing environments in Benin.
Source: WARDA (2004)

In Benin, the disaggregation by rice environment shows rainfed lowland (23552 ha) to be the dominant environment followed by upland (10407 ha) with 61 and 27% of the total rice areas, respectively (Table 1). The

estimated total number of rice-farming households by rice-growing environment presents the same trend as for the estimates rice area. Highest average household rice yields (per season) are recorded in irrigated systems (2.07 Mg ha⁻¹) and the lowest on uplands (1.51 Mg ha⁻¹).

Table 1-Rice area, number of rice farming-households and average rice yield by rice environment in Benin

Rice environment	Distribution of area (ha)	Number of rice-farming households	Average yield (Mg ha ⁻¹)
Irrigated	4798	8594	2.07
Upland	10407	20033	1.51
Lowland	23552	43765	1.83

Source: Diagne et al. (2013)

Soil carbon stock and regulation

Soil carbon stock

Soil carbon stock is estimated at 1580 Pg of carbon in the top 1 meter depth against 610 Pg C in the vegetation and 750 Pg C in the atmosphere (Figure 3) (IPCC, 2013). Soil carbon stock represents two times the amount of carbon stored in the atmosphere in the form of CO₂ and more than two times the amount of carbon stored in the vegetation. Soil is therefore a major compartment of terrestrial carbon stock. Tropical soils store approximately 40% of this total, with tropical evergreen forests being the largest reservoir of soil carbon (Jobbágy & Jackson, 2000). Soil carbon stock is influenced by

climate condition, soil properties, vegetation, land use and soil management (Gamboa & Galicia, 2012).

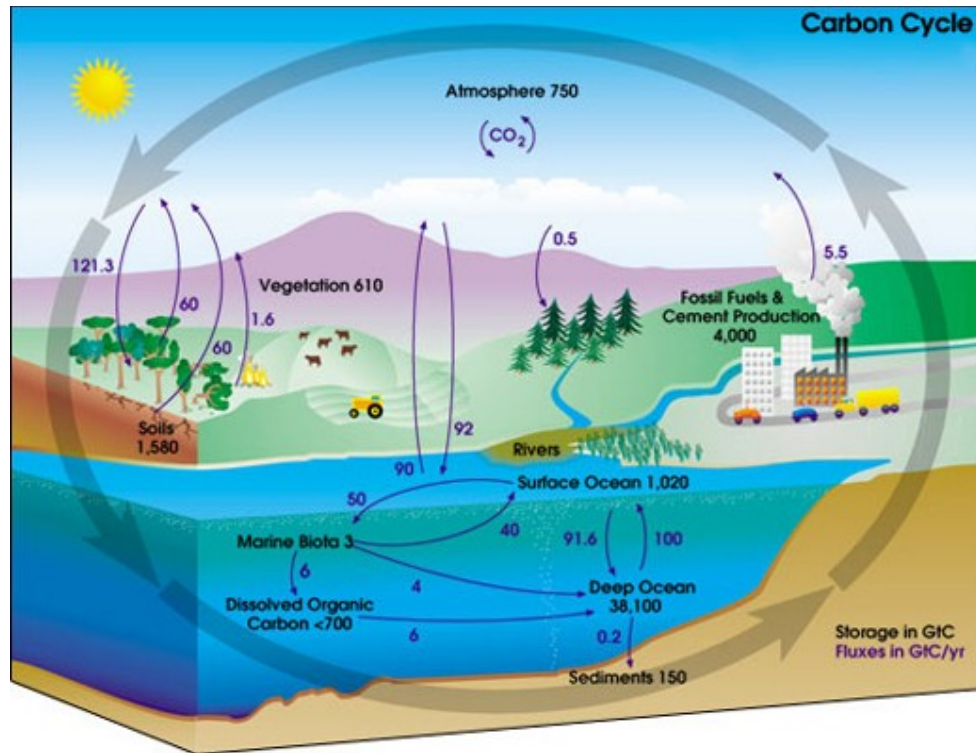


Figure 3: Carbon cycle.
Source: IPCC (2013)

Carbon cycle in terrestrial ecosystems

The increase in atmospheric CO₂, the main greenhouse gas, is driven by the emission of 5.5 gigatons (Gt) of carbon per year from fossil fuels and industrial activity and an additional 1.6 Gt per year from deforestation (Schimel, 1995). Terrestrial ecosystems and oceans absorb some of these emissions, but on average, 3.3 Gt of carbon accumulate in the atmosphere each year (Figure 3). The terrestrial absorption is the small difference between the large amounts of carbon exchanged between terrestrial ecosystems and the

atmosphere (about 120 Gt of carbon per year in each direction). This difference results in a net terrestrial carbon sink of about 2 Gt per year (IPCC, 2013).

Carbon cycle in terrestrial ecosystems is composed of carbon fluxes from the atmosphere to the terrestrial biosphere (biomass and soil). The most important fluxes are those from respiration and photosynthesis (Figure 3). These two fluxes regulate the balance of soil carbon stock. Plants assimilate carbon from the air through the process of photosynthesis by integrating atmospheric CO₂ into their own biomass (leaves, woods, roots, flowers and fruits). The outgoing fluxes of CO₂ from terrestrial ecosystems occur through plant respiration (leaf and root) and decomposition of organic matter by microorganisms.

Soil organic carbon and crop yield

Soil organic carbon (SOC) is the main constituent of soil organic matter which plays a fundamental role in the overall behavior of soils and agro-ecosystems that they support: storage and providing water and nutrients for plants, stimulating soil biological activities, improving soil physical and chemical qualities, etc. (Figure 4). Soil organic matter has a nutritional function as it serves as a source of N, P, and S for plant growth through its mineralization (Grandy & Neff, 2008). It has a biological function as it affects the activities of microfloral and microfaunal organisms. It serves as a source of energy for both macro- and microfaunal organisms. Numbers of bacteria, actinomycetes and fungi in the soil are related in a general way to soil organic

matter (Waldrop & Firestone, 2004). Earthworms and other faunal organisms are strongly affected by the quantity of plant residue material returned to the soil (Filley, Nierop, & Wang, 2006). Soil organic matter has physical and chemical functions as it promotes good soil structure, aeration, retention of moisture and increasing buffering and exchange capacity of soils (Schmidt et al., 2011). Soil organic matter also plays an indirect role in soil through its effect on the uptake of micronutrients by plants and the performance of herbicides and other agricultural chemicals. Thus, the content of soil organic carbon is generally regarded as the main indicator of soil quality, both for their agricultural and environmental functions. Soil carbon stocks and crop yields are positively correlated. Bationo, Kihara, Vanlauwe, Waswa, and Kimetu (2007) showed that maintaining or increasing soil carbon stocks can sustain the yields of crops in the tropics.

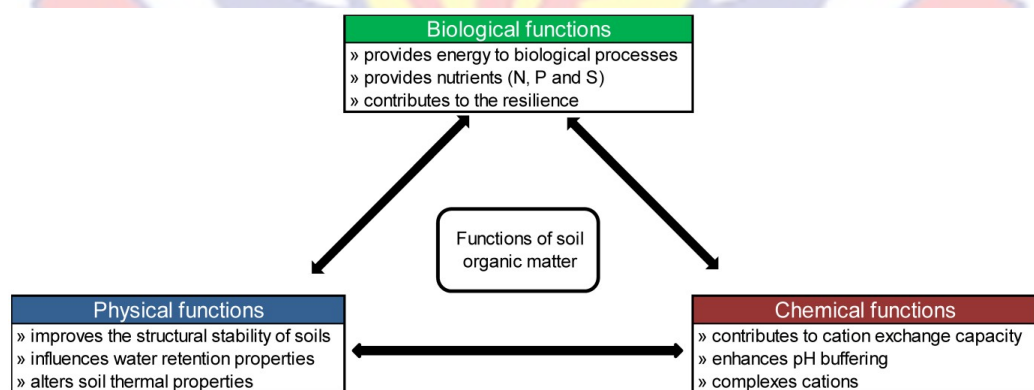


Figure 4: Functions of soil organic matter.

Source: Bationo et al. (2007)

Evolution of soil carbon stock with soil cultivation

Studies have shown a decrease in soil carbon stock with soil cultivation (Deen & Kataki, 2003). Results obtained from long-term

experiments have substantially improved knowledge on the decrease in soil productivity with the decrease in SOC due to a continuous cropping with no return of crop residues and other organic inputs. Soil carbon stock in tropical agro-ecosystems decreases sharply during the first years after soil cultivation and equilibrium is reached after about twenty years (Kintché, Guibert, Sogbedji, Lévêque, & Tiftonell, 2010). Management practices, soil and climate conditions are the major causes of soil carbon depletion. Houghton (1995) indicated that clearing forests for new agricultural land causes a release of carbon to the atmosphere. The carbon initially held in trees and other vegetation is released through burning or through decomposition of above- and belowground plant material left in the soil at the time of clearing. Even if the productivity of the new agricultural land is as high as it was in the forest, lower crop production accumulates as litter; most of it is harvested and subsequently consumed or respired. The level towards which organic pools tend under cultivation suggested that the decay rates of soil carbon were in order of magnitude higher under cultivation than under forest. Soil organic matter can thus be considered as de-protected under cultivation (Balesdent, Bernard, Arrouays, & Chenu, 1998). Hence, the process of the conversion from forest to crop and management afterward reduces carbon input from litter and enhances the carbon output via breaking the protection of soil organic matter. Reicosky (1997) indicated that there was potential for using the soil as a sink for carbon through improved soil and tillage management even though intensive tillage would cause large gaseous losses of carbon. For example, Aslam, Choudhary, and Saggarr (1999) found that adoption of no-tillage could

protect soils from biological degradation and maintain soil quality as compared with plough tillage management after land use change from forest to crop.

Soil respiration

Definition of soil respiration

Soil respiration is defined as carbon dioxide (CO₂) released from soil to the atmosphere via the combined activity of (1) roots (root respiration), and (2) micro-and macro-organisms decomposing litter and soil organic matter (heterotrophic respiration) (Figure 5) (Sulzman, 2005). Soil respiration refers to the production of carbon dioxide when soil organisms respire. This includes respiration of plant roots, rhizosphere, microbes and fauna. Soil respiration is a key ecosystem process that releases carbon from the soil in the form of CO₂. CO₂ is acquired from the atmosphere and converted into organic compounds through the process of photosynthesis. Plants use these organic compounds to build structural components. When plant respiration occurs belowground, in the roots, it adds to soil respiration. Over time, plant structural components are consumed by heterotrophs. This heterotrophic consumption releases CO₂ and when this CO₂ is released by belowground organisms, it is a component of soil respiration.

Soil respiration is a critical ecosystem process that regulates carbon cycling (Hanson, Edwards, Garten, & Andrews, 2000). At the global scale, soil respiration releases carbon at a rate that is more than one order of magnitude larger than the anthropogenic emission. The soil pool from which

soil respiration releases carbon is more than two times the atmospheric pool. Thus, a small change in soil respiration can seriously alter the balance of atmosphere CO₂ concentration. To predict changes in the carbon cycle in response to global change, soil respiration has to be carefully studied (Luo & Zhou, 2010).

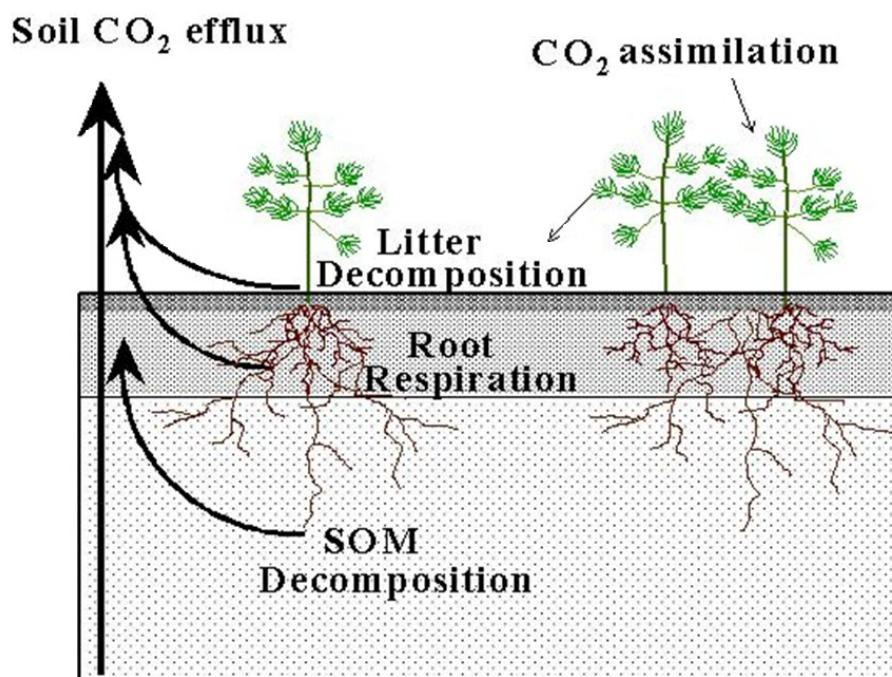


Figure 5: Components of soil CO₂ emission: autotrophic (root) and heterotrophic (microbial) respiration.

Source: Sulzman (2005)

Soil respiration and climate change

Soil respiration becomes relevant to climate change because the CO₂ released from soil respiration is one of the greenhouse gases (IPCC, 2013). The greenhouse gases permit incoming solar radiation to reach the surface of the earth but restrict the outward flux of infrared radiation. They absorb and

reradiate the outgoing infrared radiation, effectively storing some of the heat in the atmosphere. In this way, greenhouse gases trap heat within the atmosphere, resulting in climate warming near the earth's surface (Friedlingstein, Dufresne, Cox, & Rayner, 2003). The increased concentration of greenhouse gases in the atmosphere enhances the absorption and emission of infrared radiation. The atmosphere's opacity increases so that the altitude from which the earth's radiation is effectively emitted into space becomes higher. Because the temperature at higher altitudes is lower, less energy is emitted, causing a positive radiative forcing. To counteract this imbalance, the temperature of the surface-troposphere system would have to increase by 1.2 °C, in the absence of other changes. Complex feedbacks in the climate system (e.g., via clouds and their interactions with radiation) are predicted to amplify the temperature increase from 1.2 to 4.5° C (IPCC, 2001). In addition to feedback loops within the climate system, the atmosphere interacts with the biosphere through climate-carbon cycle loops. The terrestrial ecosystems presently absorb approximately 2 Pg C yr⁻¹. As atmospheric CO₂ concentration continues to increase at the "business-as-usual" emission scenario (IPCC, 1992), the land biosphere will take up an average of 7.5 Pg C yr⁻¹ by the end of the 21st century without the coupled climate-carbon cycle feedbacks (IPCC, 2013). Rising CO₂ concentration in the atmosphere enhances greenhouse effects, likely resulting in global warming. The global warming could substantially stimulate respiration, resulting in more release of CO₂ to the atmosphere to trap heat. Thus, the climate system and the global carbon cycle form a positive feedback loop to reinforce each other. An

understanding of responses of soil respiration to global warming is now urgently needed in order to evaluate uncertainty in global climate change projections (Friedlingstein et al.).

Process of CO₂ production in soil

Soil respiration involves several processes, including CO₂ production in the soil and CO₂ transport from the soil to the atmosphere. Soil respiration releases gaseous CO₂ molecules that are produced by roots, soil microbes, and soil fauna within soil and litter layers. The CO₂ produced by the living tissues is a by-product of metabolisms that yield energy and/or carbon intermediates needed for the maintenance, growth, ion uptake and reproduction of organisms. According to sources of carbohydrate substrate supply, CO₂ production in the soil can be attributed to root respiration, microbial respiration in rhizosphere, decomposition of litter, and oxidation of soil organic matter. Soil fauna may contribute a nontrivial proportion of respiratory fluxes in an ecosystem, but as the portion of CO₂ production by soil fauna has not been well quantified, this section will not describe the respiration of soil fauna in detail (Luo & Zhou, 2010).

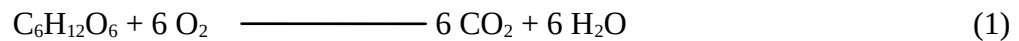
Biochemistry of CO₂ production processes

CO₂ can be produced through several biochemical pathways, the most common being the tricarboxylic acid (TCA) cycle (the citric acid cycle, also known as the Krebs cycle). Other CO₂ production processes include the fermentation of glucose to organic acids and methanotroph to oxidize methane. The fermentation happens in anaerobic environments such as

wetlands, waterlogged areas, and anaerobic microsites within soil particles, whereas the TCA cycle and methanotroph occur in aerobic conditions.

Tricarboxylic acid (TCA) cycle

Under aerobic conditions in the presence of oxygen, respiration generates energy by oxidizing sugars. The overall chemical reaction for the oxidation of glucose (or other carbohydrates) to carbon dioxide can be described as:



This process yields 2870 kJ mol⁻¹ glucose. Since respiration occurs in the presence of oxygen, this process is also called aerobic respiration of organic compounds (Lambers, Chapin, & Pons, 1998).

Biochemically, the overall processes of aerobic respiration are carried out through glycolysis, the pentose phosphate pathway, the TCA cycle, and the electron transport pathway. The oxidative pentose phosphate pathway is located in the plastids, and its primary function is to produce intermediates (e.g., amino acids and nucleotides) and nicotinamide adenine dinucleotide phosphate (NADPH) for the biosynthesis of tissue. The electron transport pathways are in the inner mitochondrial membrane associated with electron transfer and oxidative phosphorylation. CO₂ and adenosine triphosphate (ATP) production occur mainly in the glycolysis pathway and the TCA cycle. Glycolysis occurs in both the cytosol and plastids that convert glucose, via phosphoenolpyruvate (PEP), into pyruvate and malate. Pyruvate is the primary

product of glycolysis in animals and microbes, whereas plant cells convert PEP mostly to malate (Lambers et al., 1998).

Oxidation of one glucose molecule in glycolysis generates two molecules of pyruvate or malate. Glycolysis produces two molecules of ATP when pyruvate is the product, and it has no net production of ATP when malate is the end-product. The production of malate in plant cells through glycolysis also incorporates one molecule of carbon dioxide. The malate and pyruvate formed in the cytosol are imported into the mitochondria, where the TCA cycle occurs to oxidize pyruvate and malate. Complete oxidation of one molecule of pyruvate results in three molecules of CO₂, four molecules of nicotinamide adenine dinucleotide (NADH), one molecule of flavine adenine dinucleotide (FADH₂), and one molecule of ATP. Complete oxidation of one malate molecule yields one additional molecule of CO₂ and NADH, which fully compensates the need of CO₂ during the synthesis of oxaloacetate and the need of NADH in the reduction of oxaloacetate in glycolysis. Overall, the oxidation of one molecule of glucose during the glycolysis and TCA cycle produces the same amount of CO₂, regardless of whether pyruvate or malate is the intermediate product (Rocha et al., 2010).

The malate that is imported into the mitochondria is oxidized partly via malic enzyme and partly via malate dehydrogenase. The reaction with malic enzyme produces pyruvate and CO₂. Pyruvate is then oxidated in the TCA cycle, so that malate is regenerated. The reaction with malate dehydrogenase generates oxaloacetate, a substrate of the TCA cycle. The energy and intermediates produced by respiratory processes are used to sustain plant

growth, while the by-product, CO₂, is transported through the mesophyll and intercellular spaces before being released at the root or microbial surface (Grafahrend-Belau, Schreiber, Koschützki, & Junker, 2009).

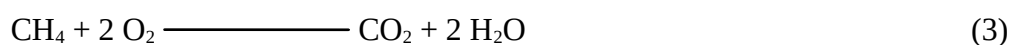
The rate of respiration at the biochemical level is regulated by a combination of energy demand, substrate availability, temperature, and oxygen supply. In general, respiration positively responds to energy demand to meet energy requirements for the growth, maintenance, and transport processes. When tissues grow fast, take up ions rapidly, and/or have a fast turnover of proteins, they generally have a high rate of respiration. When substrate supply is low, however, the respiratory pathways become substrate-limited. In the long run, the respiratory capacity is adjusted through the gene transcription for respiratory enzymes to balance the demand for respiratory energy with the supply of respiratory substrate. Respiratory processes of roots respond strongly to short-term changes in temperature and generally acclimate to long-term changes in temperature (Atkin & Tjoelker, 2003).

Other CO₂ production processes in soil

When oxygen concentration is low, aerobic respiration is inhibited and anaerobic respiration takes place. The anaerobic respiratory processes occur during fermentation, which converts glucose (or other sugar compounds) to organic products. Fermentation uses internally produced organic electron donors and acceptors and is inefficient in energy production. Fermentation has multiple pathways, some of which produce CO₂ as a product; many others do not produce CO₂. For example, the pathway of fermentation of glucose to

ethanol produces two molecules of CO₂. The chemical reaction can be described by the equation 2 (Gulati, Kohlmann, Ladisch, Hespell, & Bothast, 1996):

Methanotrophs generate a trace amount of CO₂ by oxidizing methane (CH₄) in aerobic environments (Lidstrom, 1992):



This reaction occurs in the surface layers of wetland soils, unsaturated upland soils, and other aerobic conditions. Methanogens can use acetate as substrate during fermentation in anaerobic conditions to generate CO₂:



However, methanogens can also use CO₂ as an electron acceptor to produce methane:



Methanogens are a group of anaerobic Archaea (Whitman, Bowen, & Boone, 1992). They are obligate anaerobic microorganisms, requiring redox potentials less than -100 mV in flooded soils. Since both acetate and hydrogen are by-products of fermentation, methanogenesis takes place in a complex food web and is strongly regulated by the organic material supply.

Root respiration

Root respiration consumes approximately 10 to 50% of the total carbon assimilated each day in photosynthesis (Lambers, Scheurwater, & Atkin, 1996). As a consequence, measured soil respiration is well correlated with fine root density along a gradient from an open area to lichen or vaccinium areas in a central Siberian Scots pine forest in Russia (Lambers et al.) and in loblolly pine plantations in North Carolina, with and without irrigation and/ or fertilization (Maier & Kress, 2000). The amount of CO₂ produced through root respiration is determined by the root biomass and specific root respiration rates. Root biomass in an ecosystem depends on ecosystem production and allocation patterns of plant species, and it varies with growth environments and seasons. Forests and *Sclerophyllous shrublands* have a root biomass of 5 kg m⁻², whereas croplands, deserts, tundra, and grasslands have a lower root biomass, usually less than 1.5 kg m⁻² (Jackson et al., 1996). Cold deserts have three times the root biomass of warm deserts.

At the individual plant level, carbohydrate allocation to root growth varies with plant species, age, and growth environments. Usually, root to shoot (root-shoot) ratio decreases with age due to ontogenic change during organ development. In general, root-shoot ratio is high under low levels of nutrient supply, low water availability in soil, and high levels of light. Effects of growth temperature and CO₂ concentration on root-shoot ratio are circumstantial, and no clear patterns have been generalized across various studies (Rogers, Prior, Runion, & Mitchell, 1996; Luo, Hui, & Zhang, 2006).

On the ecosystem scale, root allocation is usually higher in cold than in hot deserts and higher in grasslands than in forests.

Specific root respiration rate is the respiration rate per unit of root biomass, which varies greatly among species and with environmental factors. Measured respiration rates of excised roots from *Atriplex confertifolia* in north-western Utah range from 0.2 to 4.3 $\mu\text{mol kg}^{-1} \text{s}^{-1}$ (Holthausen & Caldwell, 1980). Root respiration is approximately 0.2 $\mu\text{mol CO}_2 \text{g}^{-1} \text{roots min}^{-1}$ for loblolly pine seedlings at 20 °C and decreases by 12% when plants are exposed to ozone (Edwards, 1991). Bryla, Bouma, and Eissenstat (1997) measured root respiration of *Citrus volkameriana*, which varied from 2 to 3.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the study period of 110 days. They did not conclude that root respiration increases after prolonged exposure to drought and increased soil temperature.

Specific root respiration rates reflect the need for energy from many processes, including (1) biosynthesis of new structural biomass, (2) translocation of photosynthate, (3) uptake of ions from soil, (4) assimilation of nitrogen and sulfur into organic compounds, (5) protein turnover, and (6) cellular ion gradient maintenance (Amthor, 2000). Thus, root respiration is regulated by a number of biotic and abiotic factors that are related to the status, life history, and environment of the plants (Amthor, 1991; Wang & Curtis, 2002). For example, root respiration linearly increases with root nitrogen concentration for sugar maple roots of various diameter classes collected at different soil depths in two forests in northern Michigan in late August (Pregitzer, Laskowski, Burton, Lessard, & Zak, 1998). Roots of

smaller diameter in shallower depths have higher nitrogen concentration and higher respiration rates. Similarly, root respiration is linearly correlated with nitrogen concentration for seedlings of nine boreal species grown at either 5% or 25% of full sunlight (Reich, Walters, Tjoelker, Vanderklein, & Buschena, 1998).

Slow-growing plants usually have lower specific root respiration rates but consume a much higher percentage of the photosynthetic product than fast-growing plants. This happens regardless of whether the growth rates are inherently low or are limited by nutrient supply (Van Gestel, Ladd, & Amato, 1991). However, light-induced changes in growth rates do not affect root respiration very much. Specific root respiration rates generally decrease with root longevity (Eissenstat, Wells, Yanai, & Whitbeck, 2000).

Respiration increases with temperature, resulting from the temperature sensitivity of enzymatically catalyzed reactions involved in respiration and the sensitivity of the increased ATP requirements as metabolic rates increase. The temperature stimulation of respiration also confirms the increased demand for energy necessary to support the increased rates of biosynthesis, transport, and protein turnover that occur at high temperatures. The rate of respiration at any given measurement temperature also depends on the growth temperature to which a plant is acclimated. Temperature acclimation results in homeostasis of respiration. The flexibility of root-respiratory acclimation to temperature is species-dependent.

Other environmental factors that influence respiratory processes include flooding, salinity, water stress, nutrient supply, irradiance, pH values,

and partial pressure of CO₂ (Lambers et al., 1998). Flooding inhibits root respiration except in the case of wetland plants, which have evolved mechanisms of aeration. Sudden exposure of plants to salinity or water stress often enhances their respiration due to an increased demand for respiratory energy. Long-term exposure of sensitive plants to salinity or drought gradually decreases respiration, as a result of the general decline in carbon assimilation associated with slow growth under these conditions.

When plants are grown at a low supply of nutrients, their rate of root respiration is lower than that of plants that are well supplied with mineral nutrients, due to reduced growth rates and ion uptake. Root respiration rates were lower in dry soil than in wet soil during the 110 days of study (Bryla et al., 1997). Bouma, Nielsen, Eissenstata, and Lynch (1997) found that root respiration of citrus is not affected by a soil CO₂ concentration within the range of 400 to 25,000 ppm, in contrast to earlier findings for the Douglas fir (Qi, Marshall, & Mattson, 1994).

Respiration is often conceptually separated into two components: growth respiration and maintenance respiration. Growth respiration yields the energy and building blocks (i.e., metabolic intermediates) for the biosynthesis of structural compounds. The maintenance respiration produces the energy required by the normal activities of living cells.

Rhizosphere respiration

The respiration of microorganisms is greatly stimulated by an abundance of carbonaceous materials (mucilage, sloughed-off cells, and

exudes) in the rhizosphere. The rhizosphere is a zone immediately next to the root surface with its neighboring soil, where a close plant-microbe interaction occurs. The concept of the rhizosphere was first introduced by L. Hiltner in 1904 (Richards, 1987) and describes the thin zone about 10 to 20 μm thick, surrounded by the mucilaginous layer. The chemical compounds in the rhizosphere vary from relatively simple oligosaccharides to a complex pectic acid polymer permeated by loose cellulose microfibrils. The space between the root cell walls and mineral soil particles is filled with a gelatinous material known as mucigel (Greaves & Darbyshire, 1972). The rhizosphere offers a highly favorable habitat for microorganisms. And the microbial community in this zone is usually quite distinct from that in the general soil. Interactions between plants and microorganisms in the rhizosphere play a critical role in regulating microbial activity, nutrient availability, decomposition of litter, and dynamics of soil organic matter.

Roots continuously release various substances to soil. According to the mode of release, there are three groups of rhizodeposition: (1) water-soluble exudates (sugars, amino acids, hormones, and vitamins), which leak from the root without involvement of metabolic energy; (2) secretions (polymeric carbohydrates and enzymes), which depend on metabolic processes for their release; and (3) lysates, released when cells autolyse (Lynch and Whipps, 1990). The root exudates of maize, for example, were mainly water soluble (79%). Among the water-soluble exudates, carbohydrates account for about 64%, amino acids/amides for 22%, and organic acids for 14% (Hutsch, Augustin, & Merbach, 2002).

Estimated amounts of carbon lost as exudates and secretions vary considerably with plant species, experimental facilities and sites, and measurement methods. Annual crops that grow in controlled facilities have been found to transfer 30 to 60% of their net fixed carbon to roots (Lynch & Whipps, 1990). Carbon transfers to root as exudates, as indicated by respiration, accounts for 10 to 70% of total carbon assimilation in 10 of the 11 studies (Lynch & Whipps). In general, the fraction of net carbon transferred to root is higher for perennial plants than for annual plants (Grayston, Vaughan, & Jones, 1996). The total root-derived carbon increases with the age of tree seedlings, ranging from 5% of net carbon uptake at 3 months to 21% at 19 months for chestnut trees (Rouhier, Billès, El Kohen, Mousseau, & Bottner, 1994). Hutsch et al. (2002) demonstrated with different plant species that up to 20% of photosynthetically fixed carbons are released into the soil during the vegetation period.

Most studies of root deposition were conducted in hydroponic and pot environments (Bekku, Koizumi, Oikawa, & Iwaki, 1997; Delucia, Callaway, Thomas, & Schlesinger, 1997; Groleau-Renaud, Plantureux, & Guckert, 1998). It is still not feasible to measure the amount of rhizodeposits in natural ecosystems despite their importance in regulating plant and ecosystem carbon balance. Based on the kinetics of the ecosystem carbon processes, Luo, Wan, Hui, and Wallace (2001) quantified root exudation through a deconvolution analysis of soil respiration in response to increase in carbon influx in an elevated CO₂ experiment in the Duke Forest, North Carolina. Dynamics of the

observed soil respiration in the first three years of the CO₂ fumigation suggests that root rhizodeposition is of minor importance in the loblolly pine forest.

However, root exudation may be an important pathway of carbon transfer to the rhizosphere in other ecosystems. For example, measured soil surface respiration gradually increases up to 35% by the end of a 58-day exposure of sunflower plants to elevated CO₂ compared with those in ambient CO₂ (Hui et al., 2001), implying substantial carbon transfer by root exudation.

The substances delivered from roots to the rhizosphere are decomposed primarily by bacteria. The small size and large surface-to-volume ratio of bacteria enable them to absorb soluble substrates rapidly. Thus, bacteria can grow and divide quickly in substrate-rich, rhizosphere zones. Bacteria also play an important role in the breakdown of live and dead bacterial and fungal cells. The major functional limitation results from its low mobility. Individual bacteria depend largely on the substrates that move to each one. The substrate at a particular location in the soil is supplied in one of the three major forms: diffusion, mass flow through water movement, and carry-over via root elongation. As roots grow, the rhizosphere moves, leading to successional change in the microbial community.

In general, the microbial community structure in the rhizosphere is distinct from that in bulk soil. Three genera *Pseudomonas*, *Achromobacter*, and *Agrobacterium* are common bacteria in the rhizosphere. Anaerobic bacteria are also present in the rhizosphere more frequently, probably due to greater oxygen consumption by root and microbial respiration than in the bulk soil. Bacteria growth in the rhizosphere is stimulated more by simple substrate

compounds, particularly by amino acids, than by complex organic compounds. For example, Vance and Chapin (2001) showed that microbial respiration responded more strongly to sucrose than to cellulose addition. In contrast, the rhizosphere does not influence fungi community as strongly as it influences the bacterial community. *Fusarium* and *Cylindrocarpon* are among the prominent inhabitants in the rhizosphere, but other genera, such as the zygomycetes *Mucor* and *Rhizopus*, are also represented.

Fungi mycorrhizae are the widespread microorganisms that are associated with roots of nearly all the families of plants (Smith & Read, 1997). They play a critical role in carbon and nutrient cycling in terrestrial ecosystems. According to the review by Allen (1991), mycorrhizal fungi consume 10 to 20% of net photosynthesis with a range from 5 to 85% among ecosystems. Mycorrhizae usually have short life spans (Friese & Allen, 1991) and high nitrogen concentrations (Wallander, Arnebrant, & Dahlberg, 1999), favoring decomposition of fungi tissues. Thus, carbon cycling through mycorrhizae is relatively fast. Nonetheless, mycorrhizae generate compounds such as chitin and glomalin, which are not readily decomposed and may form recalcitrant SOM (Rillig, 2004).

While a large percentage (64 to 86%) of these root-borne substances are rapidly respired by microorganisms, about 2 to 5% of the net carbon assimilation remains in soil (Hutsch et al., 2002). Under non-sterile conditions, the exuded compounds are rapidly stabilized in water-insoluble forms and preferably bound to the soil clay fraction. The binding of root exudates to soil particles also improves soil structure by increasing aggregate stability. The

release of organic materials from roots, even though it represents a small proportion of the total rhizodeposition, plays a critical role in the formation and decomposition of SOM through a rhizosphere-priming effect. Living plants can either increase by three-to fivefold or decrease by 10 to 30% the rate of SOM decomposition (Kuzyakov, 2002). Such short-term rate changes in SOM decomposition are due to the priming effect in the direct vicinity of the living roots (Cheng & Coleman, 1990; Liljeroth, Kuikman, & Vanveen, 1994). Root growth dynamics and photosynthesis intensity are the most important plant mediated factors affecting the priming effect (Kuzyakov & Cheng, 2001). Environmental factors, the amount of decomposable carbon in soil, and mineral nitrogen content also influence microbial activation, preferential substrate utilization, and the rhizosphere-priming effect.

Litter decomposition

Litter decomposition contributes to a significant amount of CO₂ production at the soil surface and in the soil (Jenny, Gessel, & Bingham, 1949; Olson, 1963). Removal of soil surface litter reduces annual soil respiration by 15% in undisturbed grassland in central California and by 27% in a lemon orchard in the adjacent disturbed site (Wang, Amundson, & Trumbore, 1999). To understand CO₂ production during litter decomposition, it is necessary to describe litter production, litter pool sizes, and the decomposition processes.

Litter production is the amount of biomass that transfers from live plant parts to litter pools per unit of time. Litter production is positively correlated with net ecosystem productivity. Except for a fraction of NPP that

is lost through fire, all the plant biomass eventually becomes litter that is delivered to the soil as dead organic matter. Measured aboveground litter fall amounts to 550 to 1200 g m⁻² yr⁻¹ in tropical forests (Vitousek & Howarth, 1991), 300 to 650 g m⁻² yr⁻¹ in a temperate forest (Johnson & Lindberg, 1992; Finzi, Allen, Delucia, Ellsworth, & Schlesinger, 2001; Ehman et al., 2002), and 140 to 400 g m⁻² yr⁻¹ in boreal forests (Buchmann, 2000; Longdoz, Yernaux, & Aubinet, 2000). In the Sonoran Desert, North America, the annual litter fall varied from 60 g m⁻² yr⁻¹ in the open desert and 157 g m⁻² yr⁻¹ in the thorn scrub to 357 g m⁻² yr⁻¹ in the most productive sites (Martinez-Yrizar, Burquez, Nuñez, & Miranda, 1999). On average, in a nine-year study in montane forests, leaf litter accounts for 65.1%, twig litter for 18.6%, and the follower/fruit litter for 14.4% (Liu, Wan, Su, Hui, & Luo, 2002). The production of woody litter tends to increase with forest age. In grassland ecosystems where the aboveground biomass production is mostly not in perennial tissues, the annual litter fall is approximately equal to annual net primary production.

Estimated global litter production ranges from 38 to 68 Pg C yr⁻¹ (Matthews, 1997). Estimates of the major input to litter production according to net primary production are highly consistent with the estimates from dominant short-term disposition. Following the approach of modeling net primary production, Meentemeyer, Box, and Thompson (1982) used actual evapotranspiration to predict global patterns of plant litter fall and estimated 54.8 Pg C yr⁻¹ as the annual production of aboveground litter fall worldwide.

Global patterns in the deposition of plant litterfall are similar to global patterns in net primary production (Esser, Aselmann, & Lieth, 1982).

Turnover of fine roots contributes a large amount of detritus to the soil in many ecosystems. The turnover quantifies the amount of deceased roots relative to the stock of live fine roots. Root turnover rates increased exponentially with mean annual temperature for fine roots in grasslands and forests, and for total root biomass in shrub lands (Gill & Jackson, 2000). On the broad scale, there is no correlative relationship between precipitation and root turnover. The average root turnover rates are slowest for entire tree root systems (10% annually), 34% for shrub land total roots, 53% for grassland fine roots, 55% for wetland fine roots, and 56% for forest fine roots. Root turnover rates decreased from tropical to high-latitude ecosystems for all plant function groups. The longevity of individual roots also correlates positively with mycorrhizal colonization and negatively with nitrogen concentration, root maintenance respiration, and specific root length (Eissenstat et al., 2000).

The balance between litter production and decomposition is the pool size of litter in an ecosystem. Litter production in tropical rainforests, for example, is among the highest (Schlesinger, 1997). However, a high rate of litter decomposition in tropical regions results in a low accumulation of litter at the forest floor. In contrast, boreal forests have a relatively low litter production but accumulate much more litter biomass at the forest floor than in the tropical forests, due to the low decomposition rate in the cold regions. Estimates of the global litter pool vary greatly, ranging from 50 to 75 Pg C at its low end (Schlesinger, 1977; Hudson, Gherini, & Goldstein, 1994;

Friedlingstein et al., 1995) to 150 to 200 Pg C at its high end (Esser et al., 1982; Potter et al., 1993; Foley, 1994). The lowest estimate of the total litter pool is 42 Pg C (Bonan, 1995), and the highest is 382 Pg C (Esser et al., 1982). Estimation of the global litter pool generally does not include coarse wood debris, which can be substantial (Harmon et al., 1986).

Litter materials have various compositions, including soluble components, hemicellulose, cellulose, and lignin. For example, aboveground maize residues are composed of 29.3% soluble compounds, 26.8% hemicellulose, 28.4% cellulose, 5.6% lignin, and the rest ash (Broder & Wagner, 1988). Woody litter from the Scots pine is composed of ethanol-soluble compounds (300 mg g^{-1}), lignin (383 mg g^{-1}), cellulose (111 mg g^{-1}), and lignin (65 mg g^{-1}) (Eriksson, Blanchette, & Ander, 1990). Different components of litter each have distinct decomposition rates. Therefore, it is important to analyze litter compositions, because litter does not decompose as whole units. Rather, individual soil microbes produce a distinct set of degradative enzymes such that a suite of soil microbes would be able to decompose various groups of organic compounds in litter.

Litter decomposition is usually measured as the mass remaining of original litter after a period of incubation either in the laboratory or in the field. The mass remaining usually decreases rapidly at the beginning of the incubation and then more slowly as the incubation time goes on. The time course of litter decomposition results from the fact that litter decomposition involves three processes: the leaching, fragmentation, and chemical alteration of dead organic matter to produce CO_2 , mineral nutrients, and remnant

complex organic compounds that are incorporated into SOM. Soluble materials are leached in the soil matrix by water. The soluble materials include free amino acids, organic acids, and sugars. Rapidly growing gram-negative bacteria specialize in labile substrates secreted by roots. Those microorganisms can rapidly take up those compounds for catabolic and anabolic activities. The water-soluble compounds that are not used by microbes can pass to soil to react with the minerals or are lost from the system in solution (Schlesinger, 1997).

Fragmentation is a process in which soil animals break down large pieces of litter. Animals in soil influence the decomposition of litter by fragmenting and transforming litter, grazing populations of bacteria and fungi, and altering soil structure. The microfauna are made up of the smallest animals (less than 0.1 mm). They include nematodes, protozoans, such as ciliates and amoebae; and some mites. Protozoans are single-cell organisms that ingest their prey primarily by phagocytosis, that is, by enclosing them in a membrane-bound structure that enters the cell. Protozoans are particularly important predators in the rhizosphere and other soil microsites that have a rapid bacterial growth rate (Coleman, 1994). Nematodes are an abundant and trophically diverse group. Each of the nematode species specializes in bacteria, fungi, roots, or other soil animals.

The chemical alternation of litter is primarily a consequence of the activity of bacteria and fungi. Those microorganisms metabolically function as chemoorganotrophs. They are generally heterotrophic and obtain carbon and energy while degrading organic compounds added to soil, including plant

residues and dead soil organisms. Those microorganisms secrete exoenzymes (extracellular enzymes) into their environment to initiate the breakdown of litter, which consists of compounds that are too large and insoluble to pass through microbial membranes. These exoenzymes convert macromolecules into soluble products that can be absorbed and metabolized by microbes (Luo & Zhou, 2010).

Microbes also secrete products of metabolism, such as CO₂ and inorganic nitrogen, and produce polysaccharides that enable them to attach to soil particles. When microbes die, their bodies become part of the organic substrate available for decomposition. Actinomycetes are slow-growing, gram-positive bacteria that have a filamentous structure similar to that of fungal hyphae. Like fungi, actinomycetes produce lignin-degrading enzymes and can break down relatively recalcitrant substrates. They often produce fungicides to reduce competition (Sulzman, 2005).

Fungi are a diverse group of multicellular organisms with an incredible array of vegetative and reproductive morphologies with different life cycles. They are more abundant, on a mass basis, in soils than any other group of microorganisms. Their biomass ranges from 50 to 500 g wet mass m⁻² (Metting, 1993). Fungi can inhabit almost any niches containing organic substrates and are thus active participants in ecosystems as degraders of organic matter, agents of disease, beneficial symbionts, agents of soil aggregation, and an important food source for humans and many other organisms. Fungi are the main initial decomposers of terrestrial dead plant material. Fungi have a network of hyphae (i.e., filaments) that enable them to

grow into new substrates and transport materials through the soil over distances of centimeters to meters. Hyphal networks enable fungi to acquire their carbon in one place and their nitrogen in another, much as plants gain CO₂ from the air and water and nutrients from the soil. Fungi that decompose litter on the forest floor, for example, may acquire carbon from litter and nitrogen from the mineral soil. Fungi are the principal decomposers of fresh plant litter, because they secrete enzymes that enable them to penetrate the cuticle of dead leaves or the suberized exterior of roots to gain access to the interior of a dead plant organ. Litter decomposition is regulated by many factors, including (1) climatic factors such as annual mean temperature, annual mean precipitation, and annual actual evapotranspiration (2) litter quality, such as N content, C : N ratio, lignin content, and lignin : N ratio; and (3) vegetation and litter types (Luo & Zhou, 2010).

Oxidation of soil organic matter

SOM is the organic fraction of the soil and usually does not include plant roots and not decayed macro animals and plant residues in soil. SOM supplies nutrients for plant growth, contributes to cation exchange capacity so as to maintain soil fertility, and improves soil structure. Recently, extensive research on SOM has been conducted to explain the potential of soil to sequester carbon in a form of organic matter (Eusterhues, Rumpel, Kleber, & Kogel-Knabner, 2003).

SOM consists of humic and non humic substances. The non humic materials are unrecognizable organic residues of plants, animals, and

microbes. They usually account for up to 20% of SOM. The remaining 80% or more of SOM are humic substances (i.e., humus), which are formed by secondary synthesis reactions. As litter undergoes biochemical alterations, micro-organisms synthesize additional compounds, some of which polymerize or condense through either chemical or enzymatic reactions. A key mechanism of humus formation appears to be through enzymatic or auto oxidative polymerization reactions involving phenolic compounds (Six, Conant, Paul, & Paustian, 2002).

Humus is a complex mixture of chemical compounds with a highly irregular structure containing aromatic rings in abundance. Thus, SOM typically has a netlike, three-dimensional structure that coats mineral particles and can be electrochemically bound to clay and metal oxides in the soil. SOM and clay minerals can undergo non enzymatic chemical reactions to form more complex compounds, which become more difficult to break down. The carbon content of humus is approximately 58%, and nitrogen content varies from 3 to 6%, giving a C: N ratio of 10-20 (Jastrow & Miller, 1997).

SOM can be separated into a few cohorts according to formation age and chemical compositions. A portion of SOM is easily decomposable, though most are stabilized by some physical, chemical, and/or biochemical protection from decomposition (Jastrow & Miller, 1997; Six et al., 2002). Physical protection is rendered by soil aggregation, which reduces contacts between chemical compounds of SOM with microorganisms, enzymes, or oxygen. Chemical protection occurs when organic materials are associated with minerals either directly or indirectly through cation bridging. Biochemical

protection results from condensation and polymerization reactions, forming organic macromolecules. The macromolecules resist decomposition, because organisms are unable to make efficient use of them or lack the enzymes to degrade them. Thus, humus tends to accumulate in soil when enzymes cannot easily degrade its irregular structure (Oads, 1989).

Breakdown of organic matter involves complex processes, including chemical alterations of organic matter, physical fragmentation, and releases of mineral nutrients. A variety of soil organisms such as microorganisms, earthworms, micro arthropods, ants, and beetles are involved in this process to perform chemical and physical changes at different stages. Organic matter breakdown is regulated by many factors, including soil moisture, thermal regimes, soil texture, bedrock type, nutrient status (cation exchange capacity), water capacity, illuviation and bioturbation rates, root penetration resistance, and the availability of oxygen to support aerobic microbial respiration. These variables tend to be coupled in such a way that soil texture becomes a useful proxy for most of them, with SOC levels negatively correlating with the particle sizes of the soil substrate. Disturbances such as deforestation, logging, agricultural and grazing practices, and biomass burning usually reduce SOC by either lessening carbon input or increasing carbon release. For example, plowing usually damages soil structure and accelerates the decomposition of SOM. Deforestation and biomass burning decrease carbon input into SOC pools. SOM consists of stable materials with a decomposition rate of 5% or less per year, depending on climatic conditions. An increase in soil temperature usually favors decomposition of humus materials. Increases in

soil aeration favor oxidative decomposition. Adequate nitrogen supply usually increases the rate of decomposition of SOM. Mechanical disturbance by cultivation also favors decomposition. Under the anaerobic environment in wetlands, swamps, or marshes, litter decomposition is greatly reduced and organic residue accumulates, eventually forming histosol, an organic soil (Bai, Han, Wu, Chen, & Li, 2005).

Processes of CO₂ transport from soil to the atmosphere

Carbon dioxide produced in soil by roots and micro- and macroorganisms transfers through soil profiles to the soil surface. At the soil surface, CO₂ is released into the air by both diffusion and air turbulence. The released CO₂ is then mixed in plant canopy, partly absorbed by photosynthesis during daytime, and mostly released to the atmosphere through a planetary boundary layer (PBL). This chapter describes CO₂ transport from the site of production in soil to the bulk atmosphere along the four segments of the soil-atmosphere continuum. The four segments are the soil, soil surface, plant canopy, and PBL. Although none of the transport processes may alter the total amount of CO₂ produced in soil, they are the fundamental mechanisms upon which most of the measurement methods for soil respiration are based. Thus, understanding the transport processes is critical for developing and evaluating measurement methodology. Transport processes are also sources of short-term fluctuation in soil surface CO₂ flux which may bias measured soil respiration values (Luo & Zhou, 2010).

CO₂ transport within soil

The soil is a heterogeneous medium of solid, liquid, and gaseous phases, varying in its properties both across the landscape and in depth. Transport of gaseous CO₂ in the heterogeneous soil is driven largely by a concentration gradient along a profile from deep layers to soil surface.

CO₂ concentration has distinct vertical profiles, high in deep soil layers and low in the surface soil layers. For example, the CO₂ concentration is from 320 to 1000 $\mu\text{mol mol}^{-1}$ in the surface and from 17500 to 32000 $\mu\text{mol mol}^{-1}$ in the deep soil at two sites in California (Lewicki et al., 2003). The CO₂ concentration in the deep soil layers could be 100 times the concentration at the soil surface, reaching 6 to 8% (Buyanovasky & Wagner, 1983). The steep vertical CO₂ concentration gradient is formed primarily from the slow upward movement of CO₂ from sources of production. Due to the vertical distributions of roots and SOM, CO₂ is produced more in the surface layer than in the deep layers by roots and soil micro- and macroorganisms along a soil profile. The majority of the CO₂ thus produced is released to the atmosphere with a small fraction that leaches into groundwater as dissolved inorganic carbonate. The upward movement of CO₂ from deep soil layers to the soil surface via diffusion and mass flow requires a gradient. Air movement in soil is a very slow process, leading to a buildup of steep CO₂ gradients in spite of the fact that the profile of CO₂ production sources is the opposite of the CO₂ concentration gradients. Another factor in the development of CO₂ concentration profile is CO₂ molecular weight that is heavier than air molecules. Naturally, CO₂ has the tendency to sink down along the soil profile.

The soil CO₂ concentration profile and its gradient vary with several factors: (1) soil texture and porosity, (2) precipitation and/or water infiltration, and (3) CO₂ production rate versus movement rate. If soil porosity is low, CO₂ concentration gradient is usually high. During the precipitation and infiltration, soil CO₂ is either forced out (degassing) or washed the vertical away, resulting in low CO₂ concentration along the profile. If CO₂ production is high, it requires a high CO₂ gradient to diffuse CO₂ to the soil surface.

The soil CO₂ profiles display a distinct seasonality. For example, the CO₂ concentration at a depth of 50 cm increases by about 4500 ppm from early June to late July in a young jack pine forest in Canada (Striegl & Wickland, 2001). It decreases to the values similar to those measured at the beginning of the growing season by mid-August. The jack pine forest has an extensive lateral root system, largely in the upper 45 cm of soil (Carroll & Bliss, 1982; Rudolph & Laidly, 1990). The strong fluctuation in the CO₂ concentration over season is driven largely by changes in soil CO₂ production.

CO₂ movement in soil occurs through a continuous network of air filled pores that connect the surface to the deeper layers of the soil, except in excessively wet or compacted conditions (Hillel, 1998). Gaseous movement within the soil takes place primarily by mass flow and diffusion. The mass flow occurs when a gradient of total gas pressure exists between zones. The entire mass of air streams from the zone of the higher pressure to that of the lower pressure. Diffusion, on the other hand, is driven by a gradient of partial pressure (or concentration) of CO₂ molecules in the air.

CO₂ release at the soil surface

While CO₂ transport along the soil profile is determined primarily by diffusivity of soil matrix and the steepness of the CO₂ gradient, CO₂ releases at the soil surface are strongly influenced by gusts and turbulence. It has long been documented that water loss at the soil surface via evaporation is strongly regulated by wind. For example, Hanks and Woodruff (1958) demonstrated that evaporation through soil, gravel, and straw mulches increases with wind velocity in a wind tunnel experiment. Benoit and Kirkham (1963) and Acharya and Prihar (1969) observed that the evaporation rate increases when air movement increases over soil columns covered by a layer of mulch.

Both barometric pressure fluctuations and pressure fluctuations caused by wind or air turbulence can alter soil gas exchange. According to the estimate by Kimball (1983), barometric pressure fluctuations can cause up to a 60% variation in the diffusion rate of gases in deep soils. Wind or air turbulence can increase gas fluxes to various degrees, according to soil surface texture. In an experiment with a specially designed vapor exchange meter, Kimball and Lemon (1971) demonstrated that pressure fluctuations caused by wind or air turbulence can increase gas exchange several times compared with diffusion through straw mulches and coarse gravels. In the silt loam soils with a low porosity, pressure fluctuations can increase gas fluxes by at least 25%. Effects of air turbulence on surface CO₂ probably occur through very shallow depths of soils. The transport coefficient for soil gas exchange typically ranges from 0.01 to 0.1 cm² s⁻¹ (Kimball, 1983). The lower limit of the transport coefficient is the molecular diffusion coefficient. Above and within plant

canopies where turbulent mixing of air is the primary mechanism for gas exchange, the transport coefficient typically ranges from 100 to 10000 cm² s⁻¹. Any turbulence at the soil surface that penetrates into soil layers will increase the effective value of the transport coefficient above this lower limit of molecular diffusion.

Measured CO₂ flux by chambers placed over the soils results mainly from CO₂ release at the soil surface. The effects of pressure inside the chamber caused by flow restrictions were first demonstrated by Kanemasu, Powers, and Sij (1974) and carefully studied by Fang and Moncrieff (1996, 1998), Lund, Riley, Pierce, and Field (1999), and Longdoz et al. (2000). Underpressurization or overpressurization of the chambers can cause large bias in measured CO₂ fluxes at the soil surface (Davidson et al., 2002). Wind outside the chamber also causes fluctuations in measured CO₂ fluxes (Lund et al., 1999). Using data from eddy-covariance measurements, Baldocchi and Meyers (1991) demonstrated that CO₂ flux rates at the soil surface increase markedly with increasing levels in the standard deviation in static pressure, suggesting a role for pressure fluctuations in regulating forest CO₂ exchange. Fluctuations are related to convective air movements in the PBL due to sensible heat flux from a warming surface (Stull, 1997). Static pressure fluctuations promote diffusion of gas through coarse soils and loose litter through pumping action (Kimball, 1983; Kimball & Lemon, 1971) and enhance fluxes of both water vapor and CO₂ from litter layers.

Synchronous changes in soil surface temperature and velocity fluctuations over the diurnal time course may strongly regulate the diurnal

cycle of soil CO₂ flux. At night cooler temperatures decrease CO₂ production and reduce turbulence, which results from the stable thermal stratification of the atmospheric surface layer. Turbulence and temperature increase during the day due to surface heating. The buildup of the convective PBL generates turbulence, while surface heating increases respiratory activity. The two modes of action promote the transfer of CO₂ effectively between the soil surface and the atmosphere during the daytime (Longdoz et al., 2000).

Factors controlling soil respiration

Substrate supply and ecosystem productivity

Respiratory release of CO₂ results from the breakdown of carbon-based organic substrates. CO₂ production by respiration has a 1:1 molar relationship with substrate consumption in terms of carbon atoms. At the ecosystem level, soil respiration is a composite of multiple processes, consuming substrates from various sources. Root respiration uses intercellular and intracellular sugars, proteins, lipid, and other substrates. Soil microorganisms consume all kinds of substrates, ranging from simple sugars contained in fresh residues and root exudates to complex humic acids in soil organic matter. Although respiratory CO₂ release is linearly proportional to substrate availability, the rate at which the substrates are converted to CO₂ varies with substrate types (Berg, Wessen, & Ekbohm, 1982). Simple sugars can be readily converted to CO₂ with short residence times. It can be very difficult for humic acids to be decomposed and converted to CO₂ with residence times of hundreds or thousands of years. Substrates with intermediate residence times include

celluloses, hemicelluloses, lignins, and phenols. The heterogeneity in substrate quality and multiple sources of supply make it extremely difficult to derive simple relationships between substrate supply and respiratory CO₂ production, which can be potentially incorporated into models.

The tight connections of soil respiration to aboveground photosynthesis have also been demonstrated by other studies. Root and soil respirations, for example, respond to aboveground biomass (Ruess, Michelsen, Schmidt, & Jonasson, 1999), availability of nutrients (Burton, Pregitzer, & Hendrick, 2000), light (Craine, Wedin, & Chapin, 1999), and other factors that govern plant carbon gain. On the other hand, the belowground environment strongly influences root growth and carbohydrate demand from the aboveground photosynthesis. The interaction between the demand for carbohydrates, as regulated by the soil environment, and the aboveground capacity to supply carbohydrates, as determined by photosynthesis, together govern the belowground carbon flux and therefore root and soil respiration. Despite the fact that ample experimental evidence demonstrates the intimate connections of soil respiration with aboveground photosynthesis, it is difficult to develop a quantitative relationship that directly links them. Indirect indices have been used to link soil respiration with aboveground substrate supply. For example, Reichstein et al. (2003) used leaf area index (LAI) as a surrogate of aboveground vegetation productivity and found strong correlations between soil respiration and LAI. In addition to the direct control of soil respiration by the aboveground photosynthesis, litter provides substantial amounts of carbon

substrate to microbial respiration. As a consequence, soil respiration usually increases with the amount of litter.

Soil respiration is also strongly regulated by carbon substrate in soil organic matter, as demonstrated by many laboratory incubation studies. For example, when Franzluebbers et al. (2001) collected soil samples from four climate regions in North America for an incubation study, they found that soil respiration correlated with the content of SOC. Regression coefficients that indicate how fast carbon in SOC is released via microbial respiration during the incubation period are much higher for soil from warm than cold regions and slightly higher for soil from dry than wet regions. Even if soil samples are from the same location, substrate availability may vary with physical environments, such as drying and freezing, and thus affect soil respiration. Rewetting air-dried soils, for example, results in a large respiratory flux directly related to the amount of amino acids and other nitrogenous material released by the drying process (Fierer & Schimel, 2003).

Temperature

Temperature affects almost all aspects of respiration processes. Biochemical and physiological studies usually demonstrate a general temperature response curve that respiration increases exponentially with temperature in its low range, reaches its maximum at a temperature of 45 to 50 °C and then declines. In the low temperature range, the maximum activity of respiratory enzymes is probably the most limiting factor. Low temperatures can limit the capacity of both soluble and membrane-bound enzymes (Atkin & Tjoelker, 2003). In the high temperature range, adenylates (adenosine

monophosphate [AMP], adenosine diphosphate [ADP], and adenosine triphosphate [ATP]) and substrate supply play a greater role in regulating respiratory flux (Atkin & Tjoelker). In extreme high temperatures, enzymes may degrade and respiratory activity becomes depressed.

A number of shapes have been proposed between temperature and soil respiration, but the most commonly used are reviewed by Kätterer, Reichstein, Andrén, and Lomander (1998), Kirschbaum (1995) and Lloyd and Taylor (1994). The simplest function is the so-called exponential Q_{10} relationship (Table 2), where the parameter Q_{10} is the factor by which soil respiration increases with a 10° C temperature increase (van't Hoff, 1898). The Arrhenius function is theoretically justified from first physicochemical principles of the underlying biochemical reactions and predicts an increasing Q_{10} towards higher temperatures (Arrhenius, 1889). Other exponential relationships have been derived from empirical field data, which imply a variation of soil respiration with temperature (Lloyd & Taylor, 1994). Since enzymes act in a certain temperature interval, all biological processes exhibit optimum temperatures. Hence, an optimum function was suggested by Kirschbaum (1995). Beyond this optimum, respiration rate decreases with temperature because enzymes start to be denatured which causes a decrease in respiration. Tuomi, Vanhala, Karhu, Fritze, and Liski (2008) concluded that all these models yield in similar results up to 30° C, but they strongly differ beyond this temperature.

Table 2-*Typical functions used for describing soil respiration in relation to temperature*

Author	Function
van't Hoff (1898)	$f(T) = a \times Q_{10}^{\frac{(T-T_{ref})}{10}}$
Arrhenius (1889)	$f(T) = a \times e^{-E_0/(RT)}$
Lloyd and Taylor (1994)	$f(T) = a \times e^{-Ea/(T-T_{min})}$
Kirschbaum (1995)	$f(T) = a \times e^{b \cdot T(1 - \frac{0.5T}{T_{opt}})}$

Source: Reichstein and Beer (2008)

Soil moisture

Soil moisture is an important factor influencing soil respiration. The common conceptual relationship states that soil CO₂ flux is low under dry conditions, reaches the maximal rate in intermediate soil moisture levels, and decreases at high soil moisture content when anaerobic conditions prevail to depress aerobic microbial activity. The optimum water content is usually somewhere near field capacity, where the macropore spaces are mostly air-filled, thus facilitating O₂ diffusion, and the micropore spaces are mostly water-filled, thus facilitating diffusion of soluble substrates. The maximal rate of soil CO₂ flux, for example, occurs at -15 kPa (50% of the water-holding capacity) in humid acrisols (Ilstedt, Nordgren, & Malmer, 2000). In the high soil moisture conditions, effects of soil water on respiration are regulated primarily by oxygen concentration. Although laboratory studies suggest the maximal rate of soil respiration at optimal soil water content, many of the field

observations suggest that soil moisture limits soil CO₂ flux only at the lowest and highest levels (Bowden, Newkirk, & Rullo, 1998; Liu et al., 2002; Xu, Baldocchi, & Tang, 2004). There may be a plateau of responses of soil respiration to a broad range of soil moisture, with steep decreases at either very low or very high soil moisture content. Soil moisture influences soil respiration directly through physiological processes of roots and microorganisms, and indirectly via diffusion of substrates and O₂. Effects of water stress on microbial growth vary with rates of biosynthesis, energy generation, and substrate uptake, as well as the nature and mode of water stress. Extreme dry conditions induce dormancy or spore formation in soil microorganisms (Schjonning, Thomsen, Moldrup, & Christensen, 2003) and/or cell dehydration (Stark & Firestone, 1995). Soil fungi are active at water potential as low as -15 MPa through bridging air-filled pores by hyphae extension, whereas bacteria are inactive below at -1.5 to -1.0 MPa. At low moisture content, bacteria maintain only a basic metabolism as in dormancy. Dormancy can result in substantial reductions in respiration per unit of biomass or reductions in total respiratory biomass.

Driven by stochastic events of rainfall, soil water content in the field is very dynamic and fluctuates over time. Right after rainfall, water infiltration recharges soil water content to a high level. In the subsequent period, water evaporation at the soil surface and transpiration from the foliage canopy gradually deplete soil water, causing a decline in soil water content. The stochastic events of rainfall and great fluctuation in soil moisture content usually result in strong variations in soil respiration in natural ecosystems,

particularly in arid regions. When soil is dry before rainfall, soil respiration is usually very low. Rainfall, even with a very small amount of water added to dry soil surfaces, can result in bursts of CO₂ releases from the soil (Xu et al., 2004). As soil moisture reduces via evapotranspiration and soil becomes dry over time after rainfall, rates of soil CO₂ flux decline. Although the temporal pattern of soil CO₂ flux is similar in response to different amounts of rainfall, the rate of CO₂ flux varies greatly. High rates of CO₂ flux occur at low soil moisture contents, presumably resulting from degassing right after an amount of water added to the soil surface. When large amounts of water are added to soil, soil moisture contents are recharged to high levels, but rates of CO₂ flux are not very high. The low rates of CO₂ flux at the high soil water contents are probably attributable to inhibition of gaseous movement in water-saturated soil soon after precipitation. As a consequence, the relationship derived from data collected within one wetting-drying cycle with different amounts of water addition is widely scattered between soil CO₂ flux and moisture (Liu et al., 2002).

During a wetting-drying cycle, multiple mechanisms regulate soil CO₂ flux. During the rainfall, water infiltration fills soil pores and replaces CO₂ highly concentrated air, resulting in degassing. Degassing is the fastest response to precipitation. It usually happens within minutes of precipitation and may last up to a few hours. In the strict sense, degassing is not soil respiration but rather releases the stored CO₂ in soil from past microbial and root respiration. Several hours to a few days after rain falls onto dry soil, microbe activities are activated, resulting in an increase of soil CO₂ flux.

Rewetting of extremely dry soil usually causes a strong increase in CO₂ emission, most likely because (1) a considerable proportion of soil microorganisms dies during drought (van Gestel et al., 1991) leading to quick decomposition of dead cells; (2) availability of organic substrates increases through desorption from the soil matrix (Seneviratne & Wild, 1985); and (3) exposure of organic surfaces to microorganisms increases (Birch, 1959). Fierer and Schimel (2003) used ¹⁴C labeling to identify carbon sources of the pulse CO₂ release after rewetting. Their results suggest that the CO₂ pulse release is generated entirely by mineralization of microbial biomass carbon. Since they did not observe substantial microbial cell lyses on rewetting, microorganisms likely mineralize the large amount of intracellular compounds in response to the rapid increase in soil water potential. They also found that drying and rewetting release physically protected soil organic matter, increasing the amount of extractable SOM-carbon by up to 200%. Several days after addition of water to dry soil, specific root respiration and root growth increase. It takes seven days for desert plants to initiate new root growth after rewet (Huang & Nobel, 1993). A couple of weeks after rainfall in arid lands, foliage becomes greener (Liu et al., 2002) and more carbohydrates are supplied to roots and the rhizosphere. Long-term effects of water availability on soil respiration are mediated largely by ecosystem production and soil formation (Raich, Potter, & Bhagawatti, 2002).

The relationship between CO₂ flux and soil water content is very complex, involves numerous mechanisms, and varies with regions and time-scales. In practice, the relationship has been described with various shapes

(Table 3). In general, the relationship between soil respiration and moisture is scattered (Liu et al., 2002) and developed mostly from observations of seasonal variation (Mielnick & Dugas, 2000) or along spatial gradients (Davidson, Verchot, Cattanio, Ackerman, & Carvalho, 2000) in water content.

Table 3-*Typical functions used for describing soil respiration in relation to soil moisture*

Author	Function
Stanford and Epstein (1974)	$f(\theta) = a \times \theta + b$
Brunnell, Tait, Flanagan, and Van Cleve (1977)	$f(\theta) = \frac{\theta}{a + \theta}$
Myers, Campbell, and Weier (1982)	$f(\theta) = a \times \frac{(\theta - \theta_b)}{(\theta_{i, opt} - \theta_b)}$

Soil oxygen

Soil respiration is depressed when soil water content exceeds optimal conditions due to limitation of oxygen (O₂). Soil O₂ environment becomes a main limiting factor of soil respiration in wetlands, flooding areas, and rainforests (Crawford, 1992). Silver, Lugo, and Keller (1999) measured soil O₂ concentration in three subtropical wet forests in the Luquillo Mountains, Puerto Rico. The annual precipitation increases from 3500 mm in the low elevation forest to 5000 mm in high elevation forest. As a consequence, the O₂ concentration decreases from 21% in the low-elevation Tabonuco forest to 13% in the mid-elevation Colorado forest to 8% at the depths of 10 cm and 6% at 35 cm in the high-elevation Cloud forest. Even in one forest, soil microsites experience low soil O₂ concentration (0 to 3%) for up to 25

consecutive weeks. Compaction and no-tillage can result in poor aeration and anaerobic conditions, reducing root and microbial respiration (Rice & Smith, 1982).

Nitrogen

Nitrogen directly affects respiration in several ways. Respiration generates energy to support root nitrogen uptake and assimilation. Uptake of one unit of NO_3^- may cost at least 0.4 units of CO_2 (Bouma, Broekhuysen, & Veen, 1996). Once NO_3^- is taken up by roots, it is reduced to NH_3 before the nitrogen can be assimilated into amino acids. Reduction of NO_3^- to NH_3 requires slightly more than 2 CO_2 per NO_3^- (Amthor, 2000). Assimilation of NH_3 into amino acids bioenergetically does not cost much. Nitrogen fixation from N_2 to NH_3 is catalyzed by nitrogenase within symbionts. It costs at least 2.36 CO_2 per NH_3 (Pate & Layzell, 1990). Nodule growth and maintenance have an additional cost for nitrogen fixation. High nitrogen content in tissues is usually associated with high protein content, resulting in high maintenance respiration for protein repair and replacement (Bouma et al., 1994). High nitrogen content is generally associated with high growth rates, leading to high growth respiration. Thus, respiration rates have been consistently observed to correlate with tissue nitrogen concentration (Burton, Pregitzer, Zogg, & Zak, 1998).

Nitrogen affects litter decomposition and thus microbial respiration in a complex pattern (Saiya-Cork, Sinsabaugh, & Zak, 2002). The mechanisms underlying nitrogen effects on decomposition remain unclear (Sinsabaugh,

Carreiro, & Repert, 2002). The oxidative activities associated with recalcitrant litter or soil organic matter are usually repressed by nitrogen, presumably because the micro decomposers of recalcitrant materials are generally adapted to low nitrogen conditions. High nitrogen availability might shift extracellular enzyme activity away from nitrogen limitation toward phosphorus limitation (Sinsabaugh et al.). Saiya-Cork et al. found that nitrogen amendment decreases phenol oxidase activity by 40% in soil and increases it by 63% in litter. Condensation of nitrogen-rich compounds with phenolics can make SOM more recalcitrant, resulting in decreases in microbial respiration. Addition of NH_4^+ salts can also inhibit microbial activity (Gulledge, Doyle, & Schimel, 1997). Nitrogen also indirectly affects soil respiration through ecosystem production. Nitrogen additions stimulate plant primary production (Vitousek & Howarth, 1991), which supplies more substrate for soil respiration. In nitrogen-sufficient or-rich environments, nitrogen fertilization could exacerbate conditions of nitrogen saturation, resulting in nitrogen leaching and runoff and causing little change in soil respiration.

Soil texture

There are 12 types of soil texture characterized on the basis of the percentages of sand, silt, and clay that they contain. Soil texture is related to porosity, which in turn determines soil water-holding capacity, water movement and gas diffusion in the soil, and ultimately its long-term fertility. Thus, soil texture influences soil respiration mainly through its effects on soil porosity, moisture, and fertility. Soil moisture and respiration correlated

significantly at sandy sites, but not at clayish sites in managed mixed pine forests in southeastern Georgia when soil water content was above the wilting point threshold (Dilustro, Collins, Duncan, & Crawford, 2005). Soil respiration at the sandy sites is suppressed during the warm, dry periods, whereas finer soil texture at the clayish sites buffers soil moisture effects on soil respiration due to a slow release of soil moisture. In three different soil mixtures from a fine sandy soil in Lake Alfred, Florida, and a silt clay loam in Centre County, Pennsylvania, respiration rates in the sandy soils after rewetting return to pre-watering levels nearly twice as fast as in the finer-textured soils, probably because lower soil water content in the sandy soils would allow CO₂ to diffuse more freely through air-filled pores (Bouma & Bryla, 2000). Soil texture also influences rooting systems and thus indirectly soil respiration. Generally, root growth is slower in soil of coarser texture (more sandy) than of finer texture (less sandy) due to lower fertility, lower unsaturated hydraulic conductivity, and lower water storage capacity. High root biomass and production result in high rates of root respiration and the associated microbial respiration in the rhizosphere (Hogberg, Nordgren, & Agren, 2002). In addition, root litter decomposition is sensitive to soil texture, with faster rates in the clay soil than in the sandy loam soil (Silver et al., 2005).

Soil pH

Soil pH regulates chemical reactions and a multiplicity of enzymes in microorganisms. A bacteria cell usually contains about 1000 enzymes; many

of these are pH-dependent and associated with cell components, such as membranes. In the soil matrix, adsorption of enzymes to the soil humus shifts their pH optima to higher values. Most of the known bacterial species grow within the pH range of 4 to 9. The fungi are moderately acidophilic, with a pH range of 4 to 6. Thus, soil pH has a marked effect on the growth and proliferation of soil microbes as well as soil respiration. Plants can acidify their rhizosphere soil by as much as two pH units due to release of organic acids in exudates and higher root uptake of cations than anions, leading to root excretion of H⁺ ions. Soils with pH 3.0 produce 2 to 12 times less CO₂ than the soils at pH 4.0 (Sitaula, Bakken, & Abrahamsen, 1995), due to the adverse effect of low pH on soil microbial activity. Production of CO₂ usually increases with pH when pH is less than 7 and decreases with pH at soil pH beyond 7 (Kowalenko, Ivarson, & Cameron, 1978). Emission of CO₂ decreases by 18% at pH 8.7 and 83% at pH 10.0 compared with that at pH 7.0 (Rao & Pathak, 1996). Xu and Qi (2001) found that pH values in the top 10 cm correlated negatively with soil CO₂ efflux, accounting for 34% of variation in soil CO₂ efflux.

Methods of measurements and estimations of soil respiration

There is nothing more important than accurate measurements of CO₂ fluxes in the development of the science of soil respiration. Without accurate measurements, the collected data could not objectively evaluate relative magnitudes of soil respiration among ecosystems, and might not use data to probe mechanisms and to understand the processes of soil respiration. Also

dependent on accurate measurements are partitioning of measured soil respiration into different source components, estimation of belowground allocation, and development of models to predict or simulate soil respiration in novel environments. This section first presents methodological challenges in measuring soil respiration, and then describes measurement methods, and finally evaluates their advantages and disadvantages.

Methodological challenges and classification of measurement methods

Accurate measurements of soil CO₂ flux are extraordinarily challenging due to the properties of CO₂ transport in a porous medium of soil. Transport of CO₂ takes place under the influence of both concentration gradients (diffusion flow) and pressure gradients (mass flow). First, the CO₂ concentration in soil is usually many times greater than that in ambient air with a steep gradient. Any measurement methods that disturb the soil CO₂ concentration and/or distort the gradient would result in serious errors. Second, the CO₂ transport from deep soil layers to the surface is driven primarily by diffusion along steep gradients. At the soil surface, CO₂ release is strongly influenced by changes in atmospheric pressure and pressure fluctuations caused by wind. Since soil is a porous medium, particularly at the soil surface where porosity is usually the highest, small changes in driving forces or mechanisms of CO₂ transport would alter the releases of CO₂ from soil. Third, soil respiration is extremely heterogeneous over time and space. It is highly challenging to sample representative spots at representative times and

accurately quantify spatial and temporal variability in soil respiration (Luo & Zhou, 2010).

To cope with the challenges in measuring soil respiration, scientists have conducted extensive research in the past several decades to develop a variety of measurement methods. Most commonly used are chamber methods, which provide direct measurements of CO₂ flux at the soil surface. Depending on the presence or absence of air circulation through chamber, chamber techniques can be categorized as either dynamic or static methods. The dynamic chamber methods allow air to circulate between the chamber and a measurement sensor, which is usually an infrared gas analyzer (IRGA), to measure CO₂ concentration in the chamber over time. Presently, the most commonly used method in laboratory and field measurements is the closed dynamic chamber (CDC) method, which operates in a fully enclosed mode on soil surface and measures changes in CO₂ concentration in the chamber over a short time. Some scientists employ the open dynamic chamber (ODC) method to measure soil CO₂ flux. This method operates in a continuously ventilated, quasi-steady-state mode to measure differential changes in CO₂ concentration as air passes over the soil surface. The closed static chamber (CSC) method isolates an amount of atmosphere from the environment during a measurement period as alkali solution or soda lime is used to trap CO₂. A rate of soil flux is then estimated from the trapped CO₂. With a static chamber, CO₂ concentration can also be measured from air samples at two or more different times during enclosure using syringe samples, which are analyzed with either

a gas chromatograph (GC) or IRGA to estimate the rate of soil CO₂ flux (Rochette & Hutchinson, 2005).

The soil respiration can be also estimated from gradients of CO₂ concentration along a soil vertical profile using the gas well (GW) method. Recently, many studies indirectly estimated soil respiration from measurements of net ecosystem exchange (NEE) of carbon made by micro meteorological methods such as eddy covariance (Baldocchi, Verma, Matt, & Anderson, 1986; Wohlfahrt et al., 2005) and Bowen-ratio/energy balance (BREB) (Dugas, 1993; Gilmanov et al., 2004). The measured NEE is ecosystem respiration at night or the difference between canopy photosynthesis and ecosystem respiration during daytime. The measured NEE is partitioned into photosynthesis, aboveground respiration, and soil respiration.

Closed dynamic chamber (CDC) method

The CDC method is to use a closed chamber to cover an area of ground surface and meanwhile allow air to circulate in a loop between the chamber and a CO₂-detecting sensor (IRGA) during the measurements. Once a closed chamber covers the soil surface, the CO₂ concentration in the chamber rises, due to release of CO₂ from beneath the soil surface (Table 4). The rate of CO₂ increase is proportional to the soil CO₂ flux. To determine the respiration rate, we usually use an IRGA to measure the increase in chamber CO₂ concentration over time. With two CO₂ concentration values measured at the starting and ending points respectively during a short time, the increment in

the amount of CO₂ in the chamber can be used to estimate the rate of soil CO₂ flux (Conen & Smith, 2000).

Chamber enclosure could increase CO₂ concentration in the upper part of the soil profile. Thus, fluxes calculated from fitting a linear equation to data of CO₂ concentrations within the chamber are less than those expected under the natural condition outside the chamber, because a proportion of the CO₂ produced is stored within the soil profile while the chamber is in place. The discrepancy caused by this effect increases with air-filled porosity and decreases with the height of the chamber (Conen & Smith, 2000). To correct the depression of CO₂ releases from soil by high CO₂ concentrations in the chamber, a nonlinear regression equation is required (Davidson et al., 2002).

For field measurements of soil respiration, a collar that exactly matches the size of the chamber is usually installed to a certain depth in the soil to reduce CO₂ leaking. The bottom edge of the soil chamber is sharpened. A foam gasket around the flange of the soil chamber provides a seal between the chamber and the collar. Pressure equilibrium between the air in the chamber and the surrounding air is maintained by a tube or relief vent. Air is mixed in the chamber using a diaphragm air-sampling pump that circulates air through the chamber at a certain flow rate, depending on chamber design. Chamber air is usually withdrawn at the top of the soil chamber, passes through an IRGA for continuous measurements of CO₂ concentration, and reenters the chamber through an air-dispersion ring at the bottom. Chamber CO₂ concentration should not be allowed to build up too far above ambient CO₂ concentration, or the flux will be underestimated because soil CO₂ flux decreases with chamber

CO₂ concentration. The best estimate of the flux is obtained when concentration inside the chamber is equal to that outside. Thus, the system design should make measurements of CO₂ flux around ambient CO₂ concentration. The commercial products are usually designed to scrub the chamber concentration to just below an ambient target and then measure CO₂ concentration as it rises to slightly above the ambient. Soil CO₂ flux can be obtained in about 1 to 30 minutes, depending on the system design and the magnitude of the soil CO₂ flux (Welles, Demetriades-Shah, & McDermitt, 2001).

Most of the commercially available instruments for measurement of soil CO₂ flux are built according to the principles of the CDC method. The soil respiration system developed by PP Systems in Hitchin, U.K., consists of the soil respiration chamber and either the Environmental Gas Monitor or Differential CO₂/H₂O Infrared Gas Analyzers. The portable CDC systems developed by the Li-Cor BioSciences in Lincoln, Nebraska, combine the Li-Cor 6200 gas analyzer with the Li 6000-09 chamber or the Li-Cor 6400 gas analyzer with the Li 6400-09 soil chamber. A newly developed, fully automated system, the Li-Cor 8100 is also based on principles of the CDC method and can repeatedly measure soil CO₂ flux at one spot over time. The system includes the analyzer control unit, which houses the system electronics, the IRGA, and the movable chamber. The portable soil respiration measurement system, SRC-1000 and SRC-2000, developed by Dynamax in Houston, Texas, consists of a console programming unit and a soil respiration chamber. As an example, the Li-Cor 6400 system with 6400-09 soil chamber

is further described here. The Li-6400-09 soil respiration chamber is equipped with a pressure relief vent. The standard chamber with a diameter of 95.5 mm and a volume of 991 cm₃ is placed on a PVC collar (diameter 103 mm, height 50 mm) installed to a soil depth of 20 to 30 mm. Air is circulated from the chamber to the IRGA and back by a mixing fan. Before each cycle of flux measurement, air in the chamber headspace is scrubbed down 10 to 20 ppm below the ambient CO₂ concentration and then allowed to rise as a consequence of CO₂ flux. During this period, at least five datum points of CO₂ concentrations are taken. This procedure can be repeated a few more times for each measurement. A measurement cycle usually lasts one to two minutes in grasslands and forests or two to five minutes in soil with very low rates of soil respiration. The flux is calculated by fitting a nonlinear curve to measured CO₂ concentrations in the chamber over time (Luo & Zhou, 2010).

Open dynamic chamber (ODC) method

The ODC method uses a differential mode to estimate CO₂ fluxes in contrast to the closed dynamic system that uses changes in CO₂ concentration over a period of time. Ambient air flows from an inlet to an outlet through chamber (Fang & Moncrieff, 1998; Iritz, Lindroth, & Gärdenäs, 1997). The air leaving the chamber is enriched in CO₂ concentration relative to the air entering the chamber, due to CO₂ release from respiration at the soil surface.

The open system with differential mode has been extensively used in study (Pumpanen et al., 2001). For example, Edwards and Riggs (2003) have developed a movable-lip chamber with the open system. A chamber is permanently installed at soil surface with a movable lip. The lip is open most of

the time. When a measurement starts, the lip closes over the chamber in response to a control signal. It remains closed for a period of several minutes while the measurement is made. During the measurement, the IRGA operates in differential mode when equivalent flow rates of reference gas (ambient air) and sample gas (air exiting chamber) are maintained with mass flow controllers. A large mixing bottle is usually used to buffer frequent changes in ambient CO₂ concentration. Once the measurement is taken, the lip opens again to allow normal drying and wetting of the soil and litter falling into the soil surface between measurements.

With the ODC method, the CO₂ flux is obtained from the difference in the amounts of CO₂ between the inlet air and the outlet air of the chamber. A difference between the inflow and the outflow rates can cause a pressure difference between the chamber and the ambient air and thus can generate additional air flow between the chamber and the soil. Even a pressure difference of 1 Pascal (Pa) can cause substantial errors in CO₂ flux measurements (Lund et al., 1999). Therefore, the design of an ODC system requires a minimal pressure difference between the chamber interior and the atmosphere to eliminate any mass flow of air into or out of the chamber. In practice, it is inevitable that the chamber is leaky to some extent during a measurement due to the porous nature of soil and pressure differences between the inside and outside of the chamber. In the past, air seals were usually achieved by maintaining a slight positive pressure within the chamber, ensuring that ambient air did not enter the chamber and dilute the air inside. Air seals may equally well be created with a slight negative pressure within

the chamber, drawing in ambient air and ensuring that no chamber air is lost (Rayment & Jarvis, 1997). The ODC system, Dynamax SRC-MV5, uses specially designed inlet and outlet fittings to ensure that there is no internal pressure gradient in the chamber. Also, accurate measurements of air flow rates through the chamber are critical for the calculation of soil respiration rates (Rayment & Jarvis).

Closed static chamber (CSC) methods

The CSC methods cover an area of soil surface with a chamber having a chemical absorbent inside to absorb CO₂ molecules within a certain time. The chemical absorbents for CO₂ trapping include alkali (NaOH or KOH) solution and soda lime, which consists of NaOH and Ca(OH)₂. The alkali solution method is probably the oldest method of soil respiration measurement, while the soda-lime method is probably the most frequently used static technique because it is inexpensive and easy to use (Grogan, 1998). Since the chamber is closed without air flow except CO₂ releases from soil, this method is sometimes also called the non-steady-state or non-through-flow chamber technique. However, the CSC methods are not restricted to the use of alkali or soda lime traps, but also include gas sampling for GC analysis or the use of CO₂ sensors (Dossou-Yovo et al., 2016).

Alkali trapping

Soil respiration is determined using alkali traps by absorbing CO₂ released from the soil into a sealed headspace chamber for a specific period of

time using NaOH or KOH solutions. At the end of the adsorption period, the total mass of CO₂ in the alkali traps is determined by titrating the NaOH or KOH solutions with a dilute HCl to a set pH value (Gupta & Singh, 1977).

The estimated rate of soil respiration using this technique varies with solution strengths, volumes, chamber sizes, absorption times, and absorption areas. An increase in the normality of NaOH from 0.25 to 0.75 N has no effect on CO₂ absorption capability when sufficient volumes (>30 ml) of NaOH are used. An increase in the absorption area of up to 19.9% of the total surface area of the ground enclosed has no effect on CO₂ absorption at 0.25 and 0.5 N alkali concentrations either. An increase in the volume of NaOH beyond 30 ml has no effect on the measured rate of soil respiration at the concentrations tested in the range of 0.5 to 2 N. However, the rate of CO₂ flux determined by the static chamber method is very sensitive to adsorption times, exhibiting a power decrease with time. The flux rates from a minicosm study decrease with absorption time from 20.3 mg CO₂ m⁻² h⁻¹ for absorption time of 1 h to 3.7 mg CO₂ m⁻² h⁻¹ for an absorption time of 48 h at temperature of 5°C (Kabwe, Hendry, Wilson, & Lawrence, 2002). Similarly, the flux rates from the mesocosm decrease from 276 mg CO₂ m⁻² h⁻¹ for the absorption time of 1 h to about 24 mg CO₂ m⁻² h⁻¹ for the absorption time of 110 h. The CO₂ flux rates with the alkali-trapping technique reported in the literature are obtained mostly under long absorption times, typically over 24 h (Kabwe et al.).

After reviewing the literature on measurements made with the CSC methods, Rochette and Hutchinson (2003) made recommendations for optimizing the design of the measurement procedure. Their recommendations

include (1) that the optimal strength of the alkali solution is 0.5 to 1.0 M; (2) that the alkali trap should have a total capacity approximately three times greater than the amount of CO₂ expected to be released during the deployment period; (3) that a 20% ratio of exposed alkali trap area to emitting soil surface area provides good absorption efficiency in many situations, but can be altered when needed to keep headspace CO₂ concentration as close as possible to the ambient level; (4) that the chamber should be non-vented and should have good seals that minimize CO₂ exchange between the chamber and its surroundings; and (5) that the deployment period should be at least 12 and preferably 24 h to minimize measurement bias due to the initial non-steady-state condition, as well as bias due to chamber-induced temperature disturbances.

Soda-lime trapping

The soda-lime technique has been used for more than 40 years to measure CO₂ fluxes from soil under field conditions. Soda lime is a mixture of sodium and calcium hydroxides that reacts with CO₂ to form carbonates. The amount of CO₂ adsorbed by soda lime in a chamber over the soil surface is determined by the gain in soda-lime dry weight during the sampling period. The increase in weight is directly related to the absorption of CO₂ with a correction factor. Protocols for its use are described in detail by Zibilske (1994). In brief, oven-dried (105° C) soda lime (1.5 to 2.0 mesh) is put in an open jar and placed on the soil surface beneath a closed chamber. Blanks that are necessary for CO₂ flux calculations are sealed in cylinders. Soda-lime traps

are removed after 24 hours, oven-dried, and reweighed to determine the amount of CO₂ absorbed.

The CO₂ adsorption rate of soda lime is rarely in equilibrium with the flux rates to be measured at the soil surface, leading to potential errors in measurements. The method tends to overestimate soil CO₂ flux in its low range and underestimate it in its high range compared with dynamic methods (Yim, Joo, & Nakane, 2002). The technique can potentially underestimate soil surface CO₂ fluxes by 10 to 100% (Haynes & Gower, 1995; Nay, Mattson, & Bormann, 1994). Thus, it becomes necessary to use calibration curves to compensate for this error (Grogan, 1998). Usually, larger errors occur for chambers that are not well designed to match the rates of soil respiration they are intended to measure (Hutchinson & Rochette, 2003).

Healy, Striegl, Russell, Hutchinson, and Livingston (1996) numerically evaluated the accuracy of measurements by the static chamber. Enclosure with a static chamber on the soil surface slows down CO₂ flux in comparison with that in the absence of the chamber, primarily resulting from distortion of the soil CO₂ concentration gradient.

To improve the accuracy of measurements, the CSC method should be designed to mix air in the chamber headspace thoroughly, minimize deployment time, maximize the height and radius of the chamber, and push the rim of the chamber into the soil to avoid leaking. The measurements with the soda-lime or alkali trapping can provide a single, integrated estimate of soil respiration over a daily time-scale that incorporates the effects of diurnal fluctuations in abiotic variables on CO₂ efflux.

Gas chromatograph (GC)

In addition to being continuously measured with an IRGA on site, gas samples can be taken from the field with syringes and brought back to the laboratory for analysis with a GC or IRGA. A variant of this method is to place an IRGA such as LiCor-7500 in the closed chamber without air circulation. The procedure of taking gas samples is similar to the CSC methods. Chambers are either newly covered on an area of ground surface or permanently installed with removable lids. The lids are opaque, to eliminate CO₂ fixation by plants in the chamber during measurements. The lids are fitted with rubber septa for syringe sampling. The chamber headspace is sampled by syringe soon after sealing the lip and at intervals every a few minutes for a short time (Gulledge & Schimel, 2000). Gas samples are usually taken with 10 mL glass syringes and stored in the sealed syringes until analysis. As samples are extracted with the needle, compensation air is simultaneously drawn into the chamber through a pressure equilibrium tube.

Gas samples in the sealed syringes are analyzed for CO₂ or O₂ concentrations (or other trace gases) using a GC (Gulledge & Schimel, 2000; Knoepp & Vose, 2002; Abnee, Thompson, Kolka, D'Angelo, & Coyne, 2004) or IRGA (Bekku, Koizumi, Nakadai, & Iwaki, 1995; 1997). A GC is a device used to separate components in a gas sample. When it is injected into a gas stream, a gas sample is swept through the packed column or the open tubular column with a thermal conductivity detector (TCD) plumbed in series. The ultrasonic detector, which is more sensitive than a TCD, is also used for CO₂

analysis. Some molecule components of air samples are slowed down more than others, so that different components exit the column sequentially.

The GC method can potentially underestimate the rate of soil CO₂ fluxes in comparison with other methods by up to 45% (Knoepp & Vose, 2002). The measurement period also significantly affects the flux rates due to decreased CO₂ releases from soil with increased CO₂ concentration inside the chamber. When the measurement period increases from 10 to 30 minutes, the flux rates are underestimated by 15% on coarse and dry fine sands and by 10% on wet fine sands (Pumpanen et al., 2001). The advantage of the GC method is that the fluxes of several gas species (e.g., CH₄, CO₂, NO_x) can be measured simultaneously from the same gas samples.

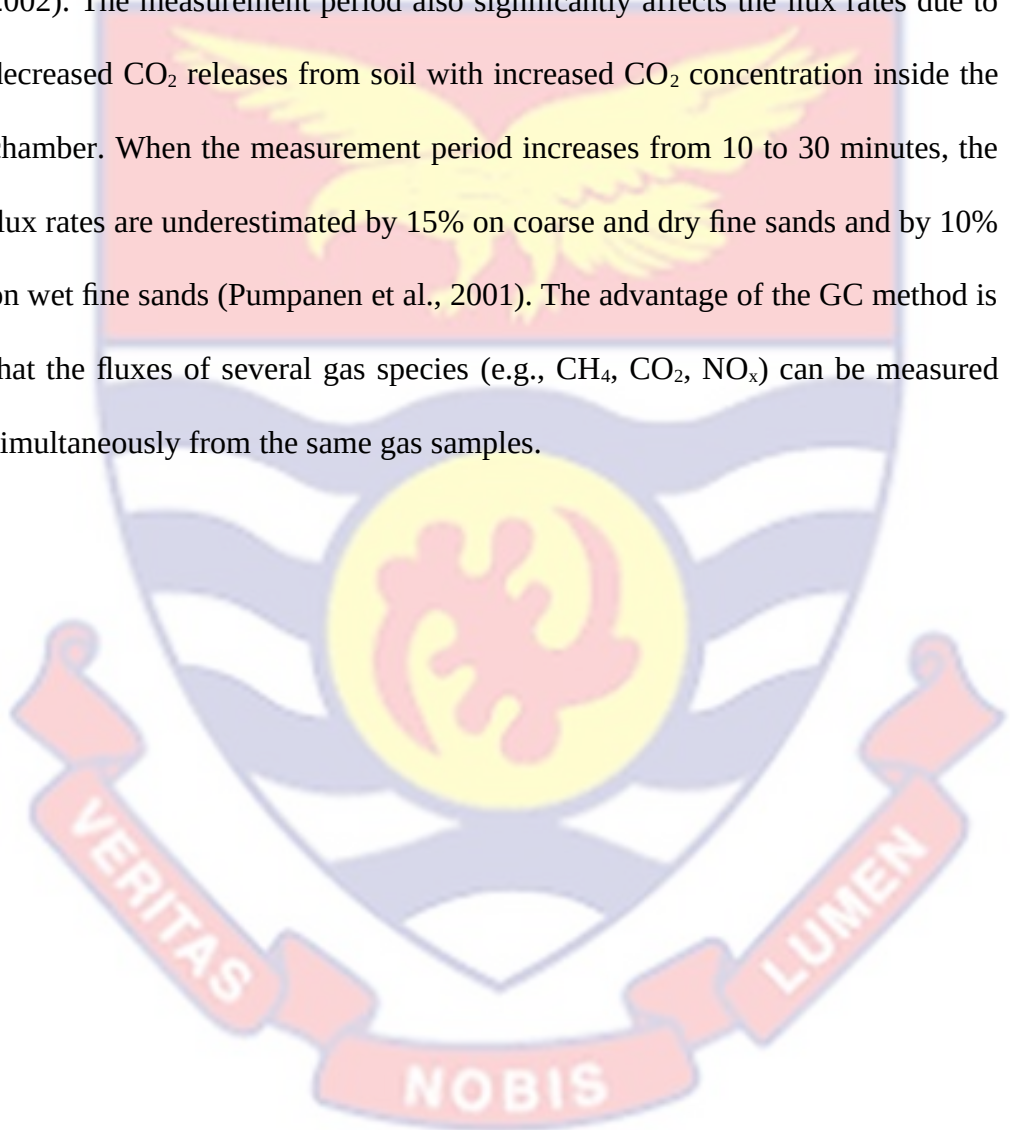


Table 4-Operating principles, advantages, and disadvantages of various measurements methods for soil respiration

Method	Operating principle	Advantage	Disadvantage
Closed chamber	dynamic Temporal gradient by building up CO2 in chamber	1. Commercially available and easy to use. 2. IRGA calibration less important due to non steady state. 3. Short measurement time and flexible for spatial sampling with a portable system.	1. Builds up CO2 concentration in chamber that distorts the gradient for diffusion. 2. Labor-intensive, with a portable systems to sample temporal variation.
Open dynamic	Differential CO2 at inlet and outlet	1. High accuracy if artifacts removed.	1. Sensitive to pressure differences inside and

chamber		2. Steady-state measurement. 3. Allows continuous measurements and high temporal variation.	outside the chamber. 2.Takes time to reach steady state in chamber. 3.Needs power supply. 4.Requires differential gas analyzer and mass flow controller.
Method	Operating principle	Advantage	Disadvantage
Closed chamber	static Stored or absorbed by base solutions or soda lime. It also includes gas sampling for GC analysis or the use of CO ₂ sensors	1.Inexpensive. 2.Potential to integrate the diurnal change. 3.Easy operation in the field and fast laboratory	1. Less accurate due to effects of CO ₂ building up on diffusion process. 2.Long enclosure/exposure times cause change

		preparation.	in microenvironments
		4.Off-site analysis of samples.	in chamber.
Gas chromatograph	Discrete temporal gradient by building up CO ₂ in chamber.	<p>1.Parallel analyses of other trace gases and isotopic composition.</p> <p>2.Easy to use and samples can be stored.</p>	<p>1.Labor-intensive to sample temporal variation.</p> <p>2.Needs a trajectory of headspace CO₂ building up to estimate respiration correctly.</p> <p>3. Requires a GC in the lab.</p>
Method	Operating principle	Advantage	Disadvantage
Gas-well	Spatial gradient by diffusion	Estimation of source depths of CO ₂ production.	Difficulty in estimation of soil and air diffusivity
Eddy-Flux	CO ₂ mixing ratios in eddies	<p>1.Nonintrusive.</p> <p>2.Measured under natural turbulent conditions.</p> <p>3.Sampling a large surface area to represent spatial heterogeneity.</p>	<p>1.Errors inherent in NEE measurements due to fetch requirements and nighttime atmospheric inversion,</p> <p>2.Difficult to partition NEE into photosynthesis,</p>

aboveground, and soil respiration.

Source: Rochette and Hutchinson (2005)



Soil Respiration Data around the world and in Africa

Hundreds of soil respiration observations have been collected globally over the decades (Figure 6). Yet, this effort has advanced very little in Africa. In 2010, the studies that had attempted to assemble data on soil respiration had not been able to suggest more than four observations for the entire African continent. For example, Chen et al. (2010), Bond-Lamberty and Thomson (2010), published global and regional databases of soil respiration with only one (Chen et al.) and four (Bond-Lamberty & Thomson, 2010) data observation points for Africa. Recently, Epule (2015) conducted a study that advanced the availability of soil respiration data in Africa by presenting all the available records. In total, 64 data points on soil respiration were recorded covering a wide range of ecosystems (Figure 7).

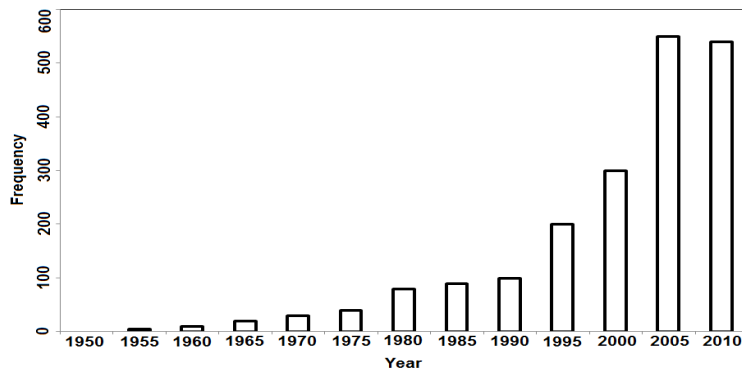


Figure 6: Soil respiration studies over time.
Source: Bond-Lamberty and Thomson (2010)

Out of the 62 observations in Africa, 25 were on forest ecosystems, 15 on agricultural ecosystems, 7 on savannah ecosystems, 7 on grassland

ecosystems, 2 on wetlands, 3 on mixed vegetation, 1 on bare ground, 1 on woody shrub and 1 on urban gardens (Cheng et al., 2010; Epule, 2015). Mixed vegetation refers to a situation in which several vegetation types co-exist in the same site, for example trees, grasses and shrubs co-existing together in mixed stands. The current shortage of adequate observations on soil respiration based on Africa is indeed a mighty gap.

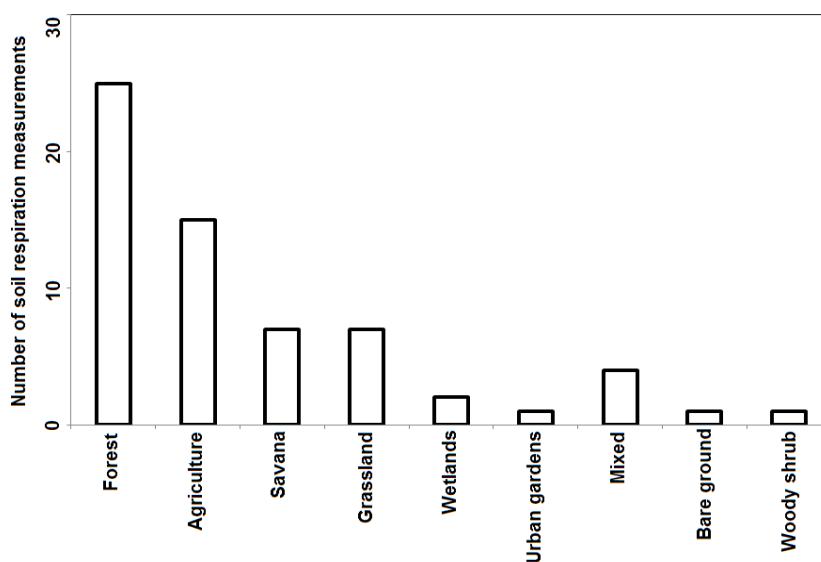


Figure 7: Main vegetation types and number of soil respiration measurements in Africa.

Source: Epule (2015)

Carbon sequestration potentials in agricultural soils

The annual soil CO₂ flux to the atmosphere is approximately 120 Gt C yr⁻¹ (IPCC, 2013). Soils play significant roles in global carbon cycle. Kimble, Lal, and Follett (2002) estimate that soils have contributed as much as 55 Pg C to the CO₂ concentration increase in the atmospheric. Although carbon

emissions from agricultural activities contribute to the enrichment of atmospheric CO₂, carbon sequestration in agricultural soils, through the use of proper management practices, can mitigate this trend. The goal to sequester soil organic carbon is to create a win-win situation to improve soil productivity, reduce unnecessary inputs, and promote sustainability.

Soil organic carbon dynamics

The basic processes of soil organic carbon dynamics can be described by the conceptual framework of the K-model developed by Feng and Li (2002) (Figure 8). Soil microbial population drives the soil organic carbon and nutrient cycles. As the plant residues or other organic materials are attacked by the soil microbial population, a portion is assimilated by soil microorganisms, becoming part of the microbial biomass. The second fraction is released to the atmosphere as CO₂. The remainder is partially transformed and may be attacked later by the microbial population. Upon death of soil microbial biomass, the soil microbial residue, along with its nutrient contents, is recycled by the succeeding generations of soil microorganisms. Residues of the dead soil microorganisms also consist of two fractions, a metabolic fraction and a structural fraction. The relative proportions of the two fractions are calculated from the overall C: N ratio of soil microbial biomass and the C: N ratio of the individual fractions. Carbon and nutrient elements in the microbial biomass are continuously recycled in the soil. Microbial growth in the soil requires specific C: N: P ratio and thus growth of microbial population is determined by balances in carbon, nitrogen and phosphorous dynamics. As the plant and

soil microbial residues undergo decomposition in the soil, the remainder, which has neither been taken up by the soil microorganisms nor released into the atmosphere as CO₂, changes in its composition, getting gradually enriched in N and P, eventually approaching that of the humus. The plant residues decompose relatively quickly in soils. Little recognizable original plant residue carbon remains in the soils after a few years. The continued cycling of microbial residues in a soil is thus the most important process affecting long-term changes in soil organic carbon (Feng & Li, 2002).

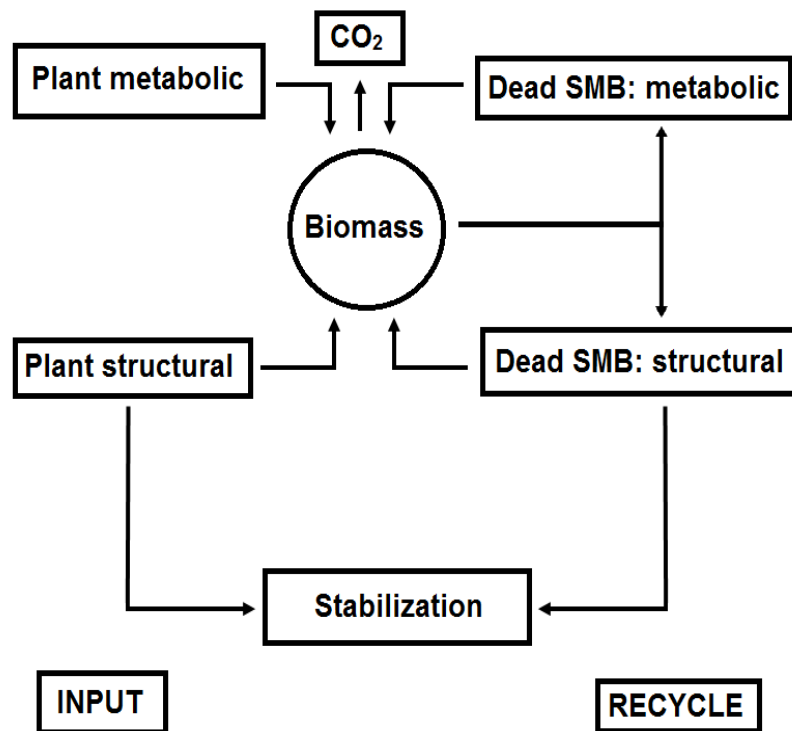


Figure 8: Soil organic carbon dynamics.
Source: Feng and Li (2002)

Practical tools to evaluate changes in soil organic carbon

Interest in maintaining and enhancing soil organic carbon stocks continuously increases, partly as a result of increasing concerns for climate change (Lal et al., 2015). Evaluation of soil carbon sequestration requires reliable tools to evaluate changes in soil organic carbon. Three options are available for this purpose: (1) direct experimental measurement and monitoring, (2) predictions with soil organic carbon models and (3) calculation of soil carbon budget. To be of practical value to the producers and farmers, these changes need to be evaluated over relatively short periods, from a single growing season to a decade (Mu et al., 2008). Change of soil organic carbon, however, is slow and occurs over much longer time periods. Direct measurement and monitoring of soil organic carbon changes over short periods must deal with uncertainties of sampling and measurement errors, and more importantly, uncertainties resulting from non-uniformity of field soils (Hanson et al., 2000).

Prediction based on models validated against available experimental evidence is another option. Most of the existing models can be broadly classified into two categories: the compartment models and the Q models. In the compartment models, soil organic carbon and associated nutrient elements are divided into kinetic compartments each characterized by a distinct decomposition rate constant. Because of the need to cope with the great diversity of time scales at which soil organic carbon and nutrient processes take place, soil organic matter is often divided into compartments with very different rate constants. Typically, for soil organic matter, three compartments

are used with time constants, i.e. $1/k$, where k is the rate constant, of approximately years, decades, and >100 years, corresponding to the broad time scales at which soil organic carbon turnover takes place. Plant material entering the soil is also divided into compartments with different rate constants to account for both the initial, fast decomposition and subsequent slow decomposition. Smith et al. (1998) conducted an extensive comparison of various compartment models. These models are complex and contain a large number of parameters for both the rate constants and the proportions of plant and organic carbon allocated into each of the compartments. In addition, parameters are also needed to describe transfer and transformation of organic carbon among the compartments during decomposition. Moreover, there is a need to specify changes in these rate constants and transfer coefficients with different soil types and environmental conditions. The fact that these parameters are often unavailable makes it necessary to estimate their values. As a result, considerable knowledge and training is required for the successful application of these models.

In the Q models, soil organic carbon is assumed to possess an attribute called 'quality', which determines the rate of its decomposition (Agren & Bosatta, 1996). The decomposition process is slowed by a continuous change in 'quality'. Unlike the compartment models, in which organic carbon is divided into separate pools or compartments with distinct properties, the Q models assume soil organic carbon as possessing a continuous distribution of 'quality'. The difficulty of these models is that the concept of 'quality' is purely conceptual and cannot be related to specific physical and chemical

properties or characteristics of soil organic carbon that can be measured experimentally (Feng & Li, 2002).

A third approach would be the calculation of soil carbon budget from carbon inputs (aboveground residue, root biomass, management related input of carbon) minus carbon outputs (carbon loss via heterotrophic respiration (R_h)). This approach is complex and requires sophisticated measuring systems, but it yields information about processes involved in carbon cycling and their temporal variability. The major challenge here is to distinguish the hetero-versus autotrophic soil respiration. Three primary methods have been used to distinguish hetero-versus autotrophic soil respiration including: integration of components contributing to in situ soil CO_2 flux, comparison of soils with or without root exclusion, and application of stable or radioactive isotope methods. Published estimates of the contribution of root respiration to soil CO_2 emission using each of these methods are presented in Table 5.

Component integration involves separation of the constituent soil components contributing to CO_2 flux (i.e., roots, sieved soil, and litter) followed by measurements of the specific rates of CO_2 flux from each component part. Rates of all component parts are then multiplied by their respective masses and summed to give an integrated total soil CO_2 emission. Ideally component integration also includes an *in situ* measurement of soil CO_2 emission for comparison. If the integrated sum of the component parts is in good agreement with measured soil CO_2 emission, then the component estimates from the data are considered valid. The distinguishing feature and potential limitation of the component integration approach is that root specific

respiration rates are measured *in vitro*. The disadvantage of the component integration approach is the impact of physically separating the components parts of the soil. Use of the component integration method forces one to deal with measured mass specific rates that may not reflect *in situ* levels. The removal of litter may modify the soil water status of the surface soil and inadvertently impact the contribution of the soil heterotrophs, and disturbance of the root soil interface raises questions about the ability of component integration to adequately capture normal rhizosphere processes.

The root exclusion method is any procedure that indirectly estimates root contribution by measuring soil respiration with and without the presence of roots. Existing root exclusion techniques may be categorized into three broadly defined areas: (1) root removal - roots are removed, soil is placed back in reverse order of removal, and further root growth is prevented by barriers, (2) trenching - existing roots are severed by trenching at a plot boundary but not removed, and a barrier is installed to inhibit future root growth, and (3) gap analysis - aboveground vegetation is removed from relatively large areas and soil CO₂ emission measurements in the gap are compared to soil CO₂ emission data of the area with vegetation. Root exclusion techniques generally result in an initial flush of CO₂ out of the soil following disturbance. Time must pass for the increased CO₂ production rate to subside, and to allow time for the diffusion rates and production rates of CO₂ to come back to equilibrium. For example, Edwards (1991) found that 2 days were required for CO₂ flux rates to stabilize after pine root removal from soil in large (24 L) pots.

Isotopic methods allow partitioning of soil CO₂ emission between root respiration and soil organic matter decomposition *in situ*, and avoid the disturbance effects. A comprehensive presentation of the application of carbon isotope techniques in environmental studies (including additional detail on methodology) can be found in Coleman and Fry (1991). Isotopic methods for estimating the relative contribution of root and soil organic matter decomposition to soil CO₂ emission can be broadly classified as: (1) pulse labelling, (2) repeated pulse labelling, and (3) continuous labelling. Either radioactive carbon-14 (¹⁴C) or stable carbon-13 (¹³C) can be used to trace the origins of soil CO₂ emission. Although all of these methods depend on mass balance, the three techniques yield slightly different types of information about plant carbon allocation and the contribution of root respiration to soil CO₂ emission (Meharg, 1994). Both the choice of an isotope method and the timing of tracer additions can be critical to interpretations of the role of the root in contributing to soil CO₂ flux. Isotope approaches have a clear advantage over other methods because they limit soil and root disturbance, but this advantage comes at a substantial increase in cost and complexity of the analyses. In situations where high costs and/or the lack of appropriate expertise might limit the use of isotope approaches, investigators might consider the root exclusion techniques which have been shown to produce comparable results (Rochette, Flanagan, & Gregorich, 1999). In this study, we used the root exclusion technique to separate hetero-versus autotrophic soil respiration.

Table 5-*Estimates of the contribution of root respiration to soil CO₂ emission (RC) and experimental approach*

Vegetation type/ Species	Approach ¹	RC (%)	Time step	Source
<i>Alopecurus/ Festuca</i>	Cint.	37-60	day	Gloser and Tesarova (1978)
<i>Brassica campestris</i>	Cint., Rexcl.	45-56%	year	Hao and Jiang (2014)
Fallow	Cint.	13-17	day	Coleman (1973)
Grass	I	10	month	Dorr and Munnich (1987)
Grass	I	98	month	Dorr and Munnich (1986)
Oil palm	Rexcl.	30-80	year	Lamade, Djegui, and Leterme (1996)
Pasture grass	Rexcl.	53	year	Robertson, Meyers, and Saffigna (1995)
Peat lands	Rexcl.	35-45	month	Silvola, Alm, Ahlholm, Nykanen, and Martikainen (1996)
Tall grass prairie	Cint.	40	year	Kucera and Kirkham (1971)
<i>Salix/Saxifraga</i>	Cint.	10	day	Nakatsubo, Bekku, Kume, and Koizumi, (1998)
Wheat/barley	I	75-95	month	Swinnen (1994)
<i>Zea mays</i>	I	35-40	day	Rochette and Flanagan (1997)
<i>Zea mays</i>	I	10-45	year	Rochette et al. (1999)
<i>Zea mays</i>	I	10-45	year	Raich and Mora (2005)
<i>Zea mays</i>	Rexcl.	25	year	Guzman and Al-Kaisi (2014)

The time step for which the data are applicable (day, month, year) are provided. ¹ Cint. = component integration, Rexcl. = root exclusion, and I = isotopic labeling approach.

Soil carbon dynamics and soil carbon budget in different rice growing environments

The dynamics of carbon in upland rice fields significantly differs from that in lowland and irrigated rice fields. In upland rice fields, the carbon accumulated in the soil is constantly released to the atmosphere due to aerobic decomposition (Nakadai et al., 1996). In lowland and irrigated rice fields, during the submerged period of rice cultivation, CO₂ emission from the soil is limited mainly due to a decrease in the heterotrophic respiration in the soil deoxidized under the flooding water and carbon fixation by algae photosynthesis. During this submerged period in lowland and irrigated rice fields, on the contrary, methane emission from the soil increases (Epile et al., 2011). In a comparative analysis of soil carbon budget between upland and paddy rice fields, Nishimura et al. (2008) found that soil carbon budgets of the paddy rice plots were positive (from +79 to +137 g C m⁻² yr⁻¹), which indicates the accumulation of carbon in the soil due to higher dry matter production by paddy rice and lower CO₂ production, while those of the upland rice plots were negative (from -343 to -275 g C m⁻² yr⁻¹) which indicates higher loss of carbon from the soil than the amount of CO₂ absorbed by the upland rice plants. The contribution of methane (CH₄) to the soil carbon budget was found as small on upland rice fields (0.02%) and on lowland rice fields (6.37%) compared with that of CO₂ dynamics. However, from the viewpoint of global warming, the contribution of CH₄ emissions becomes much higher in paddy rice fields since the global warming potential (GWP) of CH₄ is 23 times higher than that of CO₂ in a time horizon of 100 years (IPCC, 2013). The authors concluded that the paddy rice field may be a well-carbon balanced agricultural system, often resulting in a positive increase in carbon, but that effective management

practices are needed to reduce soil carbon emission in order to maintain soil carbon balance and crop productivity in upland rice agro-ecosystems.

The present study is a contribution towards understanding the effects of field management practices on soil CO₂ emission, soil carbon budget and upland rice yield for a suggestion of sustainable farming strategies (i.e. increase or no net loss of carbon) that could meet the expectancy of smallholder upland rice farmers (short term increase in grain yields).

Options for increasing carbon sequestration in West African soils

The potential for carbon sequestration in a given soil, and agroecological zone, is proportional to the original reserves present under undisturbed conditions or steady state. Options for carbon sequestration must be chosen on the basis of knowledge of the nature and likely magnitude of carbon pools in the soils of a given biome or major agroecological region and the responses of these soils to different land uses and management systems (Batjes, 1999).

Many agroecosystems are not in a steady state, but they accumulate dry matter during a number of years after which they are disturbed by fires and other drastic events, as a result of which their SOC levels often show ‘tooth-like’ cycles (Batjes, 2001). After each disturbance, a period of constant management is required in order to reach a new steady state. In this newly undisturbed soil, the organic matter content will stabilize at an equilibrium level characteristic of the permanent soil characteristics, and land use or vegetation cover and prevailing management practices. Generally, it will take at least 25 to 50 years before a new organic carbon steady state

is reached in soils (Smith, Powlson, Glendining, & Smith, 1997). This new steady state may be lower, similar or higher than the original one (Figure 9).

Human disturbance, induced by inappropriate land use and soil mismanagement, has caused widespread soil degradation worldwide. As a result, the SOC contents in many agricultural soils are now below their potential levels. There are about 494×10^6 ha of degraded soils in Africa. Main causative factors of degradation are overgrazing (49%), agricultural mismanagement (24%), deforestation (14%), and over exploitation of natural resources (13%) (Oldeman, Hakkeling, & Sombroek, 1991).

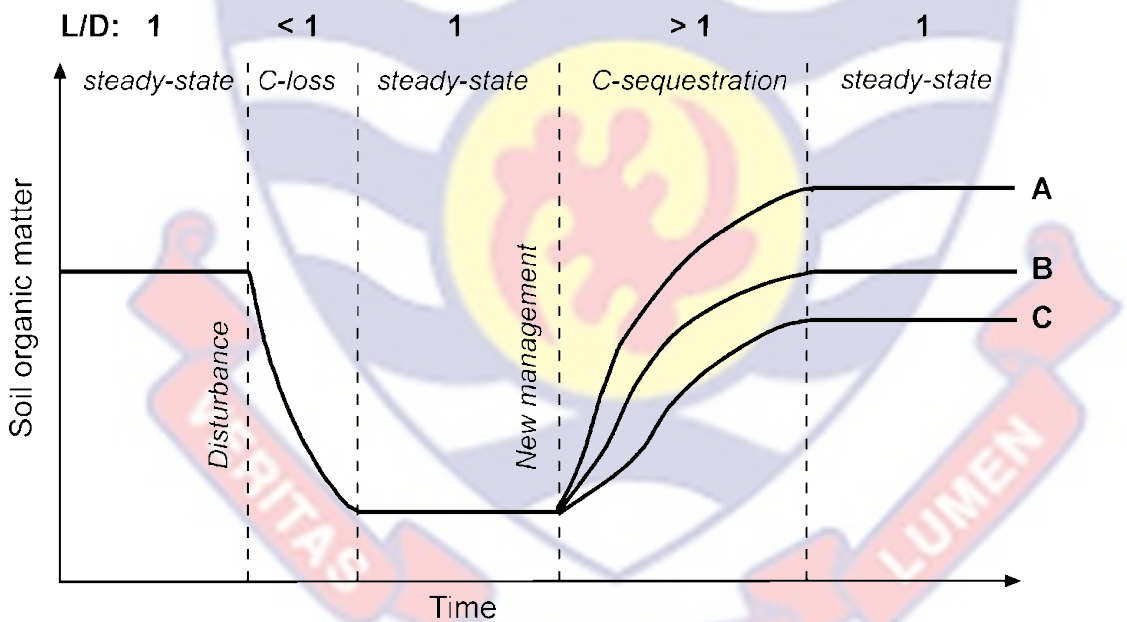


Figure 9: Conceptual model of soil organic matter decomposition/accumulation following disturbance. Scenarios: A, stabilization at above-original level; B, stabilization at original level; C, stabilization at lower than original level. L/D is the ratio of litter production over decomposition.

Source: Bajtes (2001)

Recommended management practices to build up carbon stocks in the soil are basically those that increase the input of organic matter to the soil and/or decrease the rates of soil organic matter decomposition (Lal et al., 2015). These practices will generally include a combination of the following: tillage methods and residue/stubble management; soil fertility and nutrient management; erosion control; water management; and crop selection and rotation. Sustainable management of forests and introduction of agroforestry can significantly increase the amount of carbon held in standing biomass, both above and belowground (Skjemstad, Janik, & Taylor, 1998). With respect to soil carbon sequestration, it is most desirable to fix atmospheric carbon (upon photosynthesis) in those pools having long turnover times (Buyanovsky, Aslam, & Wagner, 1994; Hassink, 1995).

Ecotechnological potential for soil carbon sequestration

Feasibility of various management practices to increase organic carbon content in the soil

Making inferences about realistic possibilities for increased carbon sequestration in the soil, through improved appropriate management, is difficult because many of the factors and processes that control the flow of carbon between soils and plants are still poorly understood (Reichle et al., 1999; Watson et al., 2000). Management practices for increasing carbon sequestration in the soil, and their inferred feasibility and associated relative carbon gains (Table 6), have been reviewed by Bruce et al. (1999). These include five broad classes: (a) reduction in tillage intensity; (b) intensification of cropping systems; (c) adoption of yield-promoting practices, including improved nutrients amendments; (d) soil/water conservation

measures, and (e) reestablishment of permanent improved perennial vegetation. While many of the practices listed in Table 6 are considered to be technically feasible by agronomists, their implementation so far has often met with limited success in maintaining or increasing soil nutrient and carbon stocks in semiarid zones of West Africa (Breman & Sissoko, 1998; Pierri, 1995; Smaling, Fresco, & DeJager, 1996). Overall, it is essential to improve the productivity and sustainability of existing agricultural lands to help reduce the rate of new land clearance, from which large amounts of CO₂ from the soil and biomass are released into the atmosphere (Paustian, Collins, & Paul, 1997).

Opportunities for carbon sequestration in the biomass and soils of terrestrial ecosystems in West Africa will vary with the agroecosystems and agroecological zone. With reference to Reichle et al. (1999), these options can be summarized as follows:

(1) On forest lands, the focus should be on belowground carbon (in stable pools), and on long-term management and utilization of standing stocks, ground cover, and litter.

(2) In the case of agricultural lands, i.e. mainly croplands and grasslands, the focus should be on increasing organic carbon in the stable SOC pools.

(3) For degraded lands, restoration can offer significant benefits in terms of carbon sequestration potential, both above the ground and in the soil.

(4) In the case of wetlands and peat lands, the focus should be on conservation and/or returning reclaimed wetlands to their natural state, keeping in mind any potential adverse environmental effects.

Carbon trading

Carbon trading, as proposed under the Kyoto Protocol, is an active process (Sampson & Scholes, 2000). So far, contracts are of variable size in terms of amount of carbon sequestered (Brown et al., 2000). Generally, contracts will be easier to monitor when the carbon sequestration potential is large, in order of 100000 t C.

Based on preliminary data, it is assumed that soil carbon sequestration at an average annual rate of 0.1 – 0.2 t C ha⁻¹ should be feasible in West Africa, provided best management practices are used and that adequate socio-economic incentives are provided (Batjes, 2001). Under these conditions, a new steady state can be reached after 25 years, corresponding to a total sequestration of 2.5 – 5 t C ha⁻¹. In order to arrive at the sequestration target of 100000 t C indicated above, about 20000 – 40000 ha of ecologically suitable land would be needed to implement a carbon sequestration project. No-tillage, the use of chemical fertilizers and crop residue cover are suggested as suitable practices to promote soil carbon sequestration (Lal et al., 2015). Several other benefits of these agricultural practices on climate change mitigation are documented mostly for the temperate ecosystem but are almost nonexistent for West Africa. The benefits from these agricultural practices are highly dependent upon the climate and soil conditions for specific cropping systems (Lu et al., 2009). These observations put to question the extent to which no-tillage, chemical fertilizers usage, and crop residue cover will improve soil carbon sequestration and rice yield on upland soils in West Africa where extremely unfavorable growth conditions prevail such as water scarcity, high temperature, and high potential evapotranspiration combined with soil degradation.

Table 6-Examples of management practices that increase organic carbon content in the soil

Management practice	Feasibility	Relative carbon gain
Cultivated land		
Use of reduced-or no-till	H	M
Improved crop nutrition and yield enhancement	H	L
Use of forages in rotation	M	M
Use of improved varieties	M	M
Use of organic amendments	M	M
Irrigation	L	H
Pasture land		
Improved grazing regime	M	M
Fertilizer application	H	M
Use of improved species/varieties	L	M
Rangeland		
Improved grazing regime	L	L
Degraded land		
Reversion to native vegetation	M	H
Establishment of fast-growing cover crops	M	H
Application of fertilizers	H	M
Application of organic amendments	L	H

Technical feasibility of management practice is expressed per unit area (L, low; M, medium; H, high).

CHAPTER THREE: MATERIALS AND METHODS

The study examined the effects of agronomic practices on soil CO₂ emission, soil carbon budget and upland rice yield. Chapter three presents the study area, the experimental design and the treatments, the methods used to estimate soil CO₂ emission, root respiration, microbial respiration and potential carbon inputs from aboveground and belowground biomass. This chapter also presents the statistical methods used to analyze the data.

Study area

Location and climate

The study was conducted in the Tetonga catchment in the district of Materi in northern Benin. The catchment is located between 1°01' E and 1°14' E and 10°42' N and 10°57' N and belongs to the Sudanian Savannah agro-ecological zone of West Africa (Figure 10).

The climate of the study area is governed by the Inter Tropical Convergence Zone (ITCZ) determined by the African monsoon that produces two annual air masses oscillations: (a) the 'monsoon' from south (equatorial Atlantic) to north (Sahara desert) determining moist conditions, and (b) the 'northeast trade' wind from north to south determining dry conditions (Sultan, Baron, Dingkuhn, Sarr, & Janicot, 2005).

Figure 11 presents the dynamism of the ICTZ in West Africa during the year. The study area is located in the domain of Sudan savannah with two seasons: the rainfall period, from May to October during which the maximum precipitation is reached in the months of August and September. The mean

annual rainfall is 1193 mm. During the rainy season, the temperature varies between 25 and 30 °C, with a relative humidity that can reach up to 97% in August. The following dry season extends over the period November until April, a period during which the temperature raises and presents its maximum in March/April. In the dry period, the maximum temperature of between 42 and 45 °C is reached and the relative humidity throughout the period is between 25 and 55% (Ahouansou, 2015).

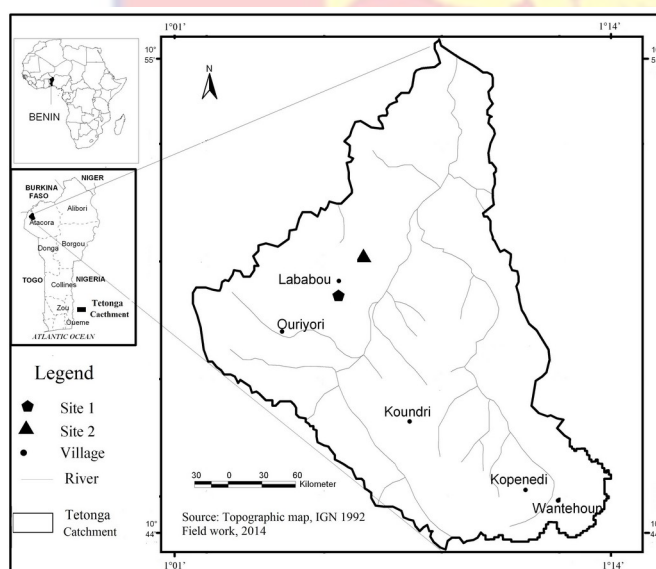


Figure 10: Location of the Tetonga catchment.

Selection of the experimental sites

In July 2013, I invited local extension agents, representatives of the organization of rice farmers of the Materi district, and technicians of the WASCAL program to a meeting in order to reflect on practical criteria which, in their experiences, could influence the selection of the experimental sites. In total, 15 rice farmers, two extension agents and two technicians of the WASCAL program attended this meeting. The farmers, drawing attention to

flooding in the lowlands and water scarcity and soil fertility problems in the uplands, requested the experiment be conducted on flat and well drained uplands. The other participants of the meeting agreed that this most problematic area would be a good experimental site. Further, the farmers and extension agents suggested that the experiment should be in a location that farmers could reach so that they can learn together and interact conveniently. After the meeting, a field trip was made in the catchment and three potential sites were identified. The final selection of the experimental site was based on the uniformity of vegetation which could be the reflection of low spatial variability in soil properties. Participants were briefed on the reasons why it was necessary to take into account the uniformity of the vegetation so as to attribute the differences between experimental plots to the treatments. In total five criteria (upland rice field, flat, well drained, adjacent to road, uniform vegetation) were agreed upon to select the experimental site. Only one site that met all the five criteria was selected. In June 2014, the experiment was reproduced in a second site that met the five criteria as the first site but showing different soil characteristics to take into account the effects of soil properties.

Soils of the experimental sites

The two experimental fields were 2 km away from each other in a gently sloping area with relative difference in elevation between the two fields of about 3 m. Site 1 was located at the upper part, and Site 2 was at the lower part of the toposequence (Figure 10). According to FAO soil taxonomy, the

soil at the upper slope was a Lixisol and at the lower slope a Gleyic Luvisol (Youssouf & Lawani, 2000).

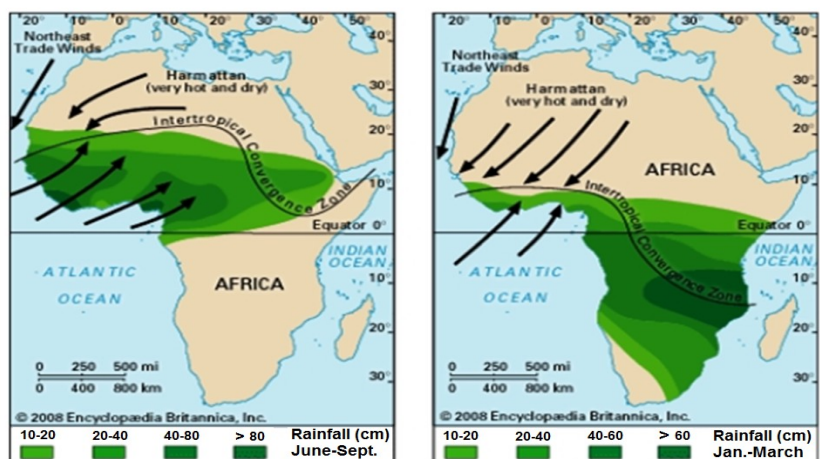


Figure 11: Intertropical Convergence Zone displacement.
Source: Matsuzaki et al. (2011)

To identify the soil constraints to plant growth, I sampled and determined the physical and chemical characteristics of surface soils (0-20 cm soil layer). Nine composite samples were taken at each site. Each sample weighed approximately 200 g. Samples were placed in plastic bags, sealed, and transported to the laboratory for analysis. Sampling was conducted in July 2013 for Site 1 and in June 2014 for Site 2. Soils were air dried and sieved to 2 mm. The sieved sample was sub-divided into two fractions: one for physical analysis and the other for chemical analysis.

Particle size distribution was determined based on the hydrometer method (Bouyoucos, 1951). The soil pH was determined using a soil-to-water ratio of 1 to 2.5. The content of soil organic carbon was determined by chromic acid digestion and the total nitrogen content by Kjeldahl digestion.

The available phosphorus content of the soil was determined using the Bray-1 method (0.5 M HCl + 1 M NH₄F). The soil potassium was extracted with 1 M NH₄-acetate and the content was determined by flame emission spectrophotometry.

Mean values of soil characteristics of the experimental sites are presented in Table 7. The scheme used in this study for the interpretation of soil chemical characteristics is presented in Table 8. Soil of Site 1 was loamy, acidic (pH < 6.1) with low organic carbon content (< 0.5%), while soil of Site 2 was a clay loam, neutral (pH 6.6 - 7.3) with medium organic carbon content (1.2%). Both sites had medium nitrogen (0.045-0.08 %), medium phosphorus (10-20 ppm) and medium potassium (0.8-1.6%) content. The two experimental sites were previously in continuous rice cultivation under manual tillage, rice straw removal and no fertilizer application.

Experimental design and treatments

The experiment consisted of twelve treatment combinations, i.e., two types of tillage, two levels of crop residue, and three levels of inorganic nitrogen (N) application. The two types of tillage were no-tillage (T₀) and manual tillage (T₁). The two levels of crop residue were no-rice straw mulch (M₀) and rice straw mulch at 3 Mg ha⁻¹ of dry rice straw (carbon content: 53.36%, nitrogen content: 0.65%, C:N ratio 82:1) (M₁). The three levels of inorganic nitrogen application were: N₀: no nitrogen application; N₁: moderate level of nitrogen (60 kg N ha⁻¹) recommended by the extension services in north Benin; N₂: high level of nitrogen (120 kg N ha⁻¹) (N₂). The use of the high level of nitrogen (120 kg N ha⁻¹) was supported by the results of a

previous study which showed that soil CO₂ emission of a Typic Fragiudult was not affected by a level of nitrogen lower than 120 kg N ha⁻¹ (Utomo, Buchari, Banuwa, Fernando, & Saleh, 2012).

Phosphorus (P) and potassium (K) fertilizers were applied in all the experimental plots to be non-limiting at 40 kg P₂O₅ ha⁻¹ and 40 kg K₂O ha⁻¹. Nitrogen, P and K were applied in the form of urea, triple superphosphate and muriate of potash, respectively. The full rate of P and K with 50% of the N was applied as basal fertilizer the day of sowing. Another 25% of the N was applied at the beginning of the tillering stage (about two weeks after germination) by top dressing. The last 25% of the N was applied at panicle initiation stage, also by top dressing. With a net plot size of 6 m x 5 m, four replications of the twelve treatment combinations were arranged in a randomized complete block design.

The no-tilled plots were treated with glyphosate to kill the fallow vegetation whereas the tilled plots were ploughed with hand hoes to the depth of 15-20 cm from the soil surface as commonly practiced in the study area. The desired rates of rice straw were applied on the plots. The rice variety NERICA14 (WAB 880-1-32-1-2-P1-HB; *O. sativa* x *O. glaberrima* interspecific progeny) was sown on 10 August, 19 July and 22 July in 2013, 2014 and 2015, respectively. Rice seeds were directly sown by hand using a dibbling stick at a row and plant-to-plant distance of 20 cm with four seeds per hill. Pre-emergence herbicide (CONDAX[®], 30% bensulfuron-methyl-W.P) was applied 24 hours after rice sowing. One week after germination, the rice plants were thinned to two plants per hill. Thereafter, weeds were hand-picked when it was necessary so as to keep the plots weed-free.

Table 7-Mean values of soil characteristics (0-20 cm) of the experimental sites

Sites	Silt (%)	Sand (%)	Clay (%)	pH	OC (%)	N (%)	P (ppm)	K (%)
Site 1	45	35	20	5.9	0.43	0.05	16.67	0.95
Site 2	28	40	32	6.77	1.20	0.08	17.99	1.44

Table 8-Interpretation scheme of soil chemical properties

Soil chemical characteristics	Interpretation scheme			
	Very low	Low	Medium	High
pH water	< 6.1	6.1 – 6.5	6.6 – 7.3	> 7.3
Organic carbon (%)	< 0.58	0.58 – 0.80	0.80 – 1.50	> 1.50
Total nitrogen (%)	< 0.03	0.03 – 0.045	0.045 – 0.08	> 0.08
Available phosphorus (ppm)	< 5	5 – 10	10 – 20	> 20
Exchangeable potassium (%)	< 0.4	0.4 – 0.8	0.8 – 1.6	> 1.6

Source: Sys, Van Ranst, Debaveye, and Beernaert (1993)

Measurement and data collection

Carbon dioxide emission measurement

The soil CO₂ emission was measured from June 2014 to May 2015 using a portable infrared CO₂ sensor (Vaisala CARBOCAP Carbon Dioxide Transmitter Series GMD20, VaisalaOy, Helsinki, Finland) with closed soil respiration chambers. Soil respiration chambers were custom-made of PVC (20 cm diameter and 18 cm height) by the workshop of the Forschungszentrum Jülich, Germany. Chambers contained a vent tube made of plastic material (length: 50 cm, inner diameter: 0.5 cm) to allow for pressure equilibration between the chamber headspace and the ambient atmosphere (Figure 12).

The soil CO₂ measurements were conducted by placing the gas-tight soil respiration chambers on PVC collars (20 cm diameter) that were inserted into the ground at least one day prior to the first measurement and remained at their position for the entire measurement period. Collars were custom-made by the workshop of the Forschungszentrum Jülich, Germany. Collars were inserted at 5 cm soil depth, leaving approximately 2 cm above the soil surface to prepare a solid foundation for the chamber and to prevent gas from escaping the chamber headspace horizontally through the soil matrix. In addition to avoiding soil disturbance, the collars had also the advantage of allowing repeated measurements in time at the same position, thereby facilitating the characterization of temporal variation of soil CO₂ fluxes (Rochette et al., 1997). Two collars were placed in the center of each plot.

During the growing season (June-October 2014), soil CO₂ emission was measured at 6 to 10 days intervals. During the non-growing season

(November 2014-May 2015), measurements were made every two weeks due to low variability in soil moisture during the dry season and the fact that soil CO₂ emission is expected to depend on soil moisture rather than temperature in Benin (Ago et al., 2014; Dossou-Yovo et al., 2016; Lamade et al., 1996; Mulindabigwi, 2005). Measurements were made between 08:00 and 11:00 h and between 15:00 and 18:00 h to take into account diurnal changes in temperature. The measurement was done just after closing the chamber and every five minutes up to thirty minutes. Air temperature inside the chamber was measured with a combined temperature and humidity transmitter (HMD 53, Vaisala Intercap® Sensor, VaisalaOy, Helsinki, Finland) connected to the soil respiration chamber. The slope of changes in CO₂ concentration with time and the air temperature inside the chamber were used to calculate the soil surface CO₂ flux according to equation 6. Two soil respiration chambers were placed on the two collars installed in the center of each plot. The mean of the soil CO₂ emission from the two chambers was considered to be the soil surface CO₂ emission for the entire plot.

$$F = \frac{dC}{dt} \times \frac{273.15}{273.15+T} \times \frac{V}{A} \times \frac{1}{V_m} \times M_c \times 60 \times 1000 \quad (6)$$

where;

F is the soil CO₂ flux (mg CO₂-C m⁻² h⁻¹); $\frac{dC}{dt}$ is the change of CO₂-concentration with time (10⁻⁶ min⁻¹), T is the temperature inside the soil respiration chamber (°C), V is the chamber volume (m³), A is the chamber base area (m²), V_m is the molar volume of air at 0 °C (0.0224 m³ mol⁻¹), M_c is the molar mass of carbon (12 g mol⁻¹), 60 is the conversion factor from minute to hour and 1000 is the conversion factor from gram to milligram.

During the study period, cumulative soil CO₂ emissions were calculated according to equation 7 (Grote & Al-kaisi, 2007):

$$M = \sum_{i=1}^n \frac{F_{i+1} + F_i}{2} \times (t_{i+1} - t_i) \quad (7)$$

where;

M is the cumulative emission of CO₂-C (mg CO₂-C m⁻²), F_i is the first CO₂ emission value (mg CO₂-C m⁻² h⁻¹) at time t_i (h), and F_{i+1} is the following value at time t_{i+1} (h); n is the total number of CO₂ emission values.

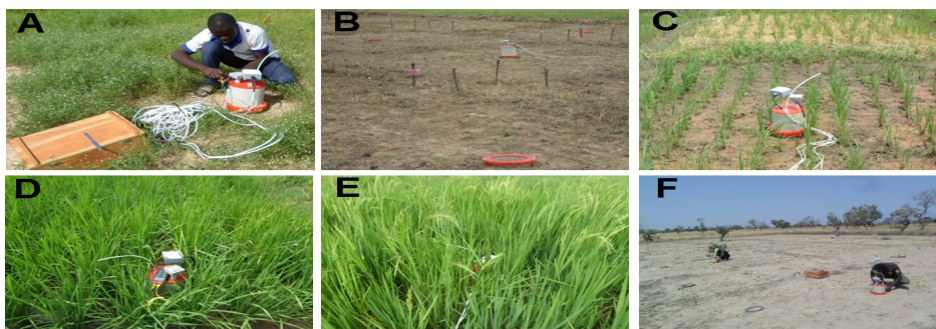


Figure 12: Soil CO₂ emission measurement (A) before land preparation, (B) at rice sowing stage, (C) at the beginning of tillering stage, (D) at the maximum tillering stage, (E) at flowering stage and (F) during the dry season.

Soil temperature, soil moisture and meteorological data measurement

Soil temperature and soil moisture were measured in the first 5 cm of soil at the same time when soil CO₂ emission was measured (Figure 13). Soil temperature was measured with a hand-held soil thermometer (Omegatete HH303 Type K J, OMEGA Engineering, Inc., Stamford, CT, USA). Soil moisture was measured with a portable TDR probe (ML2x-KIT, Delta-T

Devices Ltd., Cambridge, UK). Soil temperature and soil moisture were measured at four points close to each soil respiration chamber. The means of the soil temperature and soil moisture from the eight points (4 points close to each chamber and 2 chambers per plot) were used as central values of the plot.

Meteorological data were collected from a nearby weather station located at approximately 1 km from the experimental sites. The station was installed by the WASCAL programme. Daily measurements include rainfall and average air temperature.



Figure 13: Measurement of two soil parameters: (A) soil moisture and (B) soil temperature.

Separation of heterotrophic respiration and root respiration

To quantify percentage of root respiration (R_r) to total soil CO_2 emission (F), a root exclusion experiment was conducted (Hanson et al., 2000). In each treatment plot, soil CO_2 emission was measured between rice plants with no roots (R_h) using a stainless steel base frame (20 cm length \times 20 cm width \times 20 cm height) as a physical barrier, and with roots present (F) to

estimate contribution of R_r to total soil CO_2 emission according to equation 8 (Figure 14).

$$R_r (\%) = \frac{F - R_h}{F} \times 100 \quad (8)$$

At the end of the study, root biomass samples were collected in the root exclusion treatments to confirm that there were no rice roots present. Accordingly, by subtracting R_r contribution (%) from 100%, contribution of heterotrophic respiration (R_h) to soil CO_2 emission (F) was estimated.

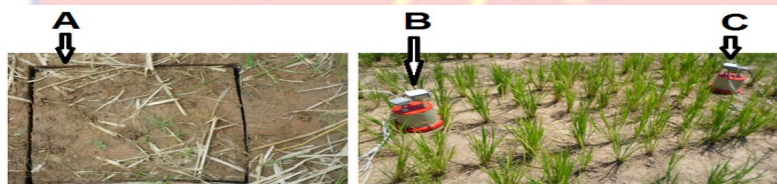


Figure 14: Root exclusion technique using (A) a stainless steel base frame inserted into soil to quantify (C) soil CO_2 emission due to organic matter decomposition from (B) total soil CO_2 emission.

Potential carbon input from aboveground and belowground plant biomass

Aboveground and belowground biomass was measured in October 2014 to quantify potential carbon inputs from plant biomass. Rice residues (aboveground biomass) were collected after grain harvest within two replicate frames of 1 m^2 each that were placed close to the center of each plot. The aboveground plant biomass was dried at $70 \text{ }^\circ\text{C}$ for 72 h, and weighed to

determine the dry matter weight (Mg ha^{-1}). Carbon content of aboveground biomass was determined by dry combustion, and the content value was multiplied by the aboveground dry matter weight to determine the potential carbon input from aboveground biomass in Mg ha^{-1} (Guzman & Al-Kaisi, 2014).

Belowground plant biomass was collected at rice harvest using a monolith sampling procedure (Shashidhar, Henry, & Hardy, 2012). Two monolith samplers (20 cm x 20 cm, 20 cm depth) were pounded into the soil in the harvested area of each plot with a sledgehammer until the top of the sampler was levelled with the soil. The soil within the monolith sampler was sampled and stored in labeled plastic bags. The roots were separated from the soil sample by flotation. The soil sample was transferred into a plastic container and mixed in water. After mixing, the soil-water-root mixture began to separate: soil settled at the bottom, large roots floated at the water surface and some roots, although not visible, floated below the water surface. The large and visible pieces of roots were picked out with forceps and transferred to a small container of clean water. The small roots floating below the water surface were collected by pouring the liquid portion over a 1.0 mm sieve. These small roots were then transferred to the small container of clean water with the large roots. Water was again added to the plastic container of the soil and the liquid portion was poured over the sieve to isolate the roots. This procedure was repeated until no more roots were collected on the sieve. After mixing the soil with water and capturing the roots on the sieve, the soil was visually examined for any remaining roots. All roots from the container were then poured over the sieve and transferred to a small labeled plastic bag. Root

samples were dried in an oven at 70 °C for 72 hours. A high-precision (milligram) balance was used to determine the dry weight of the roots. Root samples were analyzed by dry combustion for carbon content, and the content value was multiplied by root biomass to determine the potential carbon input from root (belowground) biomass in the top 20 cm soil depth in Mg ha⁻¹.

Calculation of soil carbon budget

The soil carbon budget was calculated by measuring net ecosystem productivity using a similar approach by Duiker and Lal (2000) and Kucharik, Fayram, and Cahill (2006). The soil carbon budget was calculated as the difference between carbon input due to rice straw mulch, above-and belowground biomass carbon, and carbon loss through organic matter decomposition (heterotrophic respiration) for the entire year according to equation 9.

$$SCB (Mg C h a^{-1} y r^{-1}) = C_{straw} + PAC + PBC - CR_h \quad (9)$$

where;

SCB is soil carbon budget, C_{straw} is carbon input due to rice straw mulching. C_{straw} is equal to 1.6 Mg C ha⁻¹ for rice straw mulch treatments (carbon concentration in rice straw mulch (53.36%) which was multiplied by the dry weight of rice straw mulch (3 Mg ha⁻¹)). C_{straw} is equal to 0 for non mulch treatments. PAC is potential carbon input from aboveground plant biomass, PBC is potential carbon input from root biomass, and CR_h is cumulative carbon loss via heterotrophic respiration.

Determination of rice grain yield

The effects of tillage systems, rice straw mulch and nitrogen fertilization on rice grain yield were determined during three growing seasons (2013, 2014 and 2015) at the experimental Site 1 and during two growing seasons (2014 and 2015) at the experimental Site 2. At maturity, two replicates of 1 m² were harvested in the center of each plot. Grain yields were reported at 14% moisture content.

Agronomic efficiency of nitrogen

The agronomic efficiency of nitrogen (AEN) was defined as the economic production obtained per unit of nitrogen applied (Fageria et al., 2010). It was used to evaluate optimal response of rice yield to nitrogen application under the tillage systems and the rice straw mulch rates during three growing seasons (2013, 2014 and 2015) at the experimental Site 1 and during two growing seasons (2014 and 2015) at the experimental Site 2. The AEN was calculated according to equation 10.

$$AEN = \frac{(G_f - G_u)}{N_a} \quad (10)$$

AEN is the agronomic efficiency of nitrogen (kg kg⁻¹), G_f is the grain yield of the fertilized plot (kg ha⁻¹), G_u is the grain yield of the unfertilized plot (kg ha⁻¹), and N_a is the quantity of nitrogen applied (kg ha⁻¹).

Soil CO₂ emission per unit grain yield

The amount of soil CO₂ emission per unit grain yield was calculated according to equation 11 (IPCC, 2007) in order to identify treatment combinations which can induce lower soil CO₂ emission per unit grain yield.

$$R = \frac{M}{Y} \quad (11)$$

where;

R is the amount of soil CO₂ emission per unit grain yield, M is the cumulative emission of soil CO₂ (Mg ha⁻¹), and Y is the grain yield (Mg ha⁻¹).

The amount of soil CO₂ emission per unit grain yield was calculated using the cumulative soil CO₂ emission of the period June 2014-May 2015 and the grain yield of the growing season of 2014.

Data analysis

All the statistical tests, models and figures were made with the R statistical software (R Development Core Team, 2011). An analysis of variance was performed on the treatments. Mean values were tested for significant differences by using a least significance difference (LSD). The probability level ≤ 0.05 was designated as significant.

Regression analysis was conducted on daily soil CO₂ emission and daily soil moisture and daily soil temperature of the growing and dry seasons to identify environmental factors affecting seasonal variations of soil CO₂ emission.

Stepwise regression analysis was conducted to test the effects of soil moisture, soil temperature, days after sowing (DAS) and soil CO₂ emission on the contribution of R_r to total soil CO₂ emission.

Chapter Summary

This chapter presents the materials and methods used to reach the specific objectives. Cumulative soil CO₂ for the study period was calculated following the approach of Grote and Al-Kaisi (2007). A root exclusion experiment was used to quantify the percentage of root respiration (R_r) to total soil CO₂ emission (F) (Hanson et al., 2000). Potential carbon input from aboveground biomass was estimated following the approach of Guzman and Al-Kaisi (2014). Belowground plant biomass was collected at rice harvest using a monolith sampling procedure (Shashidhar et al., 2012). The soil carbon budget was calculated as the difference between carbon input and carbon loss following the approach of Duiker and Lal (2000). The limitation from the study came from the fact that soil CO₂ emission was measured by placing the gas-tight soil respiration chambers on two collars that were placed in the center of each experimental plot. Measurements of soil CO₂ with three collars placed in the center of each experimental plot instead of two collars may capture more accurately the spatial variability of soil CO₂ emission in each experimental plot.

CHAPTER FOUR: RESULTS

The study examined the effects of agronomic practices on soil CO₂ emission, soil carbon budget and upland rice yield. This chapter presents the results obtained for each specific objective.

Effects of tillage systems, rice straw mulch and inorganic nitrogen application on soil CO₂ emission

Rainfall and air temperature

In order to examine the effects of environmental factors and agronomic practices on soil CO₂ emission, it appeared important to first describe the evolution of rainfall and air temperature during the study period. Seasonal evolutions of daily rainfall and air temperature are presented in Figure 15. The climate at the studied site was characterized by a succession of two main seasons, a dry one (November-April) and a wet one (May-October). This seasonality is depicted through the seasonal variation of rainfall. Most of total rainfall was concentrated between June and October. Daily average air temperature varied from 21 to 35° C.

Soil moisture

Soil moisture fluctuated at both sites with rainfall events. Soil moisture was approximately twice as high in no-till treatments as compared with tilled treatments from the day of land preparation to the day of sowing (Figure 16). After sowing and before rice harvest, a tillage and rice straw mulch interaction effect on soil moisture was observed. Soil moisture was lower in till and no

straw mulch (till + no-straw) treatments and higher in no till plus straw (no-till + straw) treatments. From mid-October, a steady decrease in soil moisture was recorded in all treatments due to the end of the rainy season (Figure 16). At both sites, the average soil moisture during the growing season was in the order of no-till + straw > no-till + no-straw > till + straw > till + no-straw (Figure 16). No-till treatments had on average $0.02 \text{ m}^3 \text{ m}^{-3}$ higher soil moisture than tilled treatments. Mulched treatments had on average $0.01 \text{ m}^3 \text{ m}^{-3}$ higher soil moisture than non-mulched treatments. On average, soil moisture was $0.012 \text{ m}^3 \text{ m}^{-3}$ higher at Site 2 than at Site 1 (Table 9).

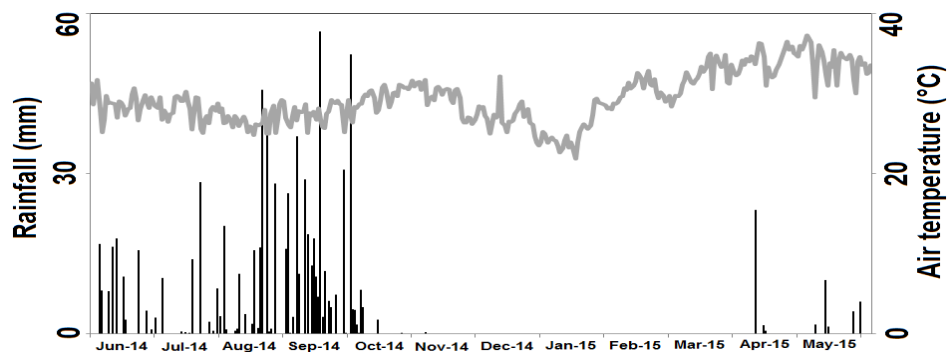


Figure 15: Seasonal evolution of daily rainfall (dark histogram) and daily average air temperature (grey line) from 01 June 2014 to 31 May 2015.

Soil temperature

Soil temperature slightly varied during the growing season (Figure 17). Seasonal mean amplitudes of $11 \text{ }^\circ\text{C}$ and $9 \text{ }^\circ\text{C}$ were found during the growing season of 2014 at Site 1 and Site 2, respectively. The lowest soil temperature ($24 \text{ }^\circ\text{C}$) was recorded at maximum rice tillering stage and panicle initiation.

The highest soil temperature was observed at the beginning and at the end of the rainy season (35 °C). During the growing season, there was a significant interaction effect of tillage and rice straw mulch on soil temperature (Table 10). Soil temperature was lower under no-tillage + rice straw mulch (26 – 27 °C) and higher under no-tillage and no rice straw mulch (30 – 32 °C).

Daily evolution of soil CO₂ flux

Figure 18 presents the daily evolution of soil CO₂ emission during the growing season of 2014 for the two sites. It was observed that soil CO₂ flux significantly increased soon after tillage from an average of 80 mg CO₂-C m⁻² h⁻¹ to 250 mg CO₂-C m⁻² h⁻¹ and decreased with time after tillage. Two weeks after tillage, no significant variation was found between tilled and no-tilled treatments. With frequent rainfall events followed by crop development, soil CO₂ flux significantly increased in all treatments and reached the maximum at the rice panicle initiation stage (end of September). The CO₂ flux in the different treatments varied during the growing season between 10 and 350 mg CO₂-C m⁻² h⁻¹ (Figure 18). On average, soil CO₂ flux was higher under manual tillage (136 mg CO₂-C m⁻² h⁻¹) than in no-tillage (82 mg CO₂-C m⁻² h⁻¹) during the growing season. There were no significant differences between soil CO₂ fluxes of the different rice straw mulch treatments early in the growing season. However, from early August, higher soil CO₂ emissions were recorded in treatments with rice straw addition. In addition, peaks of soil CO₂ emission were generally higher in fertilized treatments compared with non-fertilized treatments. During the dry season, soil CO₂ emissions continued to vary after harvest between treatments till February when emissions were near zero and

no differences were found between treatments (Figure 19). Soil CO₂ emissions remained very low in March but significantly increased to an average of 85.2 and 96.2 mg CO₂-C m⁻² h⁻¹ at Site 1 and Site 2, respectively following the first rains recorded at the beginning of April after five dry months. Soil CO₂ emissions decreased again to an average of 40.2 mg CO₂-C m⁻² h⁻¹ in May 2015 (Figure 19).

Table 9-Average soil moisture and soil temperature at 0 – 5 cm depth of the growing season of 2014 (June-November) of the tillage systems, rice straw mulch and nitrogen levels at the experimental sites

Treatment	Soil moisture (m ³ m ⁻³)	Soil temperature (°C)
Site 1	0.132 a	28.7 a
Site 2	0.144 b	28.5 a
LSD (main site effect)	0.005	ns
Tillage systems (T)		
No-tillage (T0)	0.148 a	28.7 a
Manual tillage (T1)	0.128 b	28.9 a
LSD (main T effect)	0.004	ns
Rice straw (M)		
No straw	0.133 a	30.0 a
3 Mg ha ⁻¹ of rice straw	0.143 b	27.6 b
LSD (main M effect)	0.005	0.95
Nitrogen levels (N)		
0 kg N ha ⁻¹	0.138 a	29.5 a
60 kg N ha ⁻¹	0.139 a	28.7 a
120 kg N ha ⁻¹	0.137 a	28.2 a
LSD (main N effect)	ns	ns

Numbers followed by different letters in a column within a set are significantly different at $p \leq 0.05$. ns: not significant.

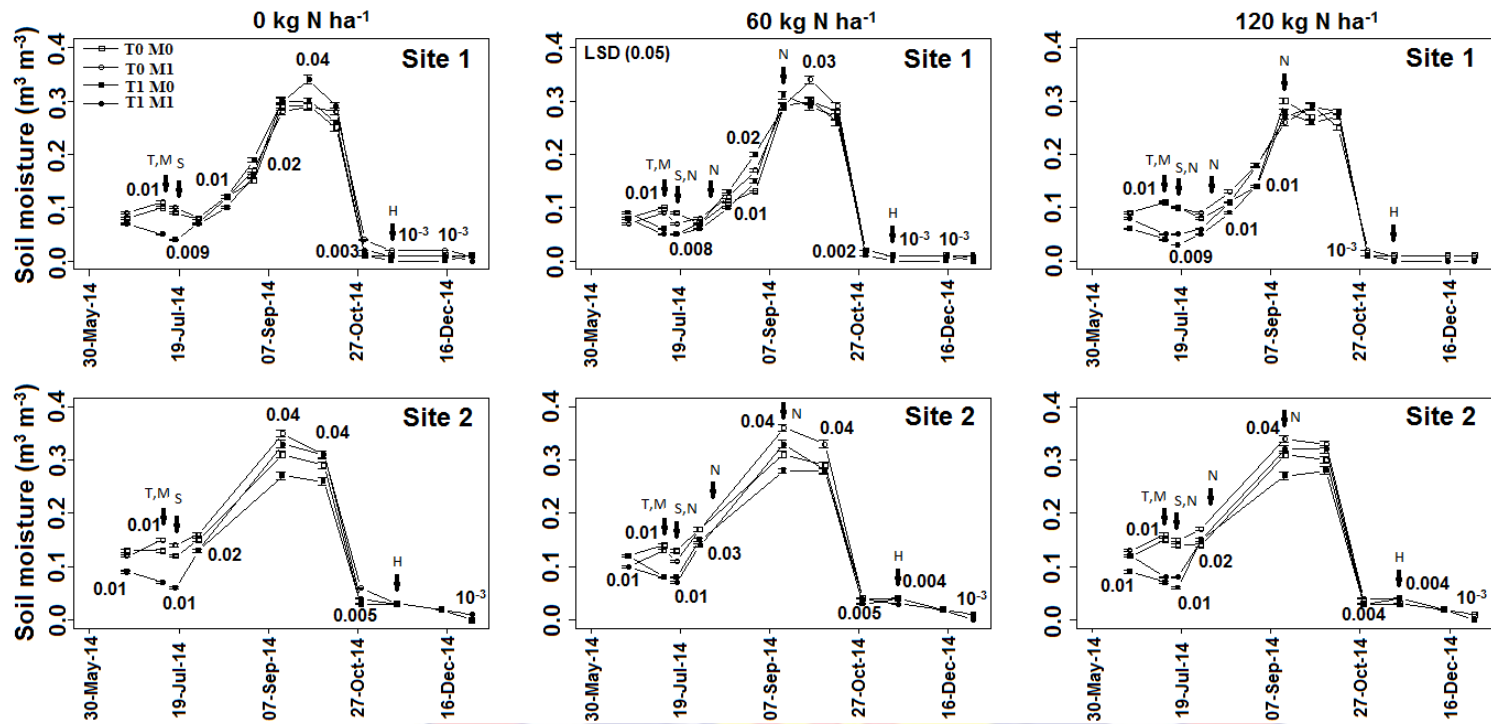


Figure 16: Tillage and rice straw mulch effects on daily soil moisture at different nitrogen fertilization levels during the growing season of 2014 at the experimental Sites 1 and 2.

T: tillage, M: application of rice straw mulch, S: sowing, N: nitrogen fertilizer application, H: harvest. LSD values at specific periods indicate significant differences at $p \leq 0.05$ between treatments; and if no value is shown then the difference is not significant. The error bars represent the standard error.

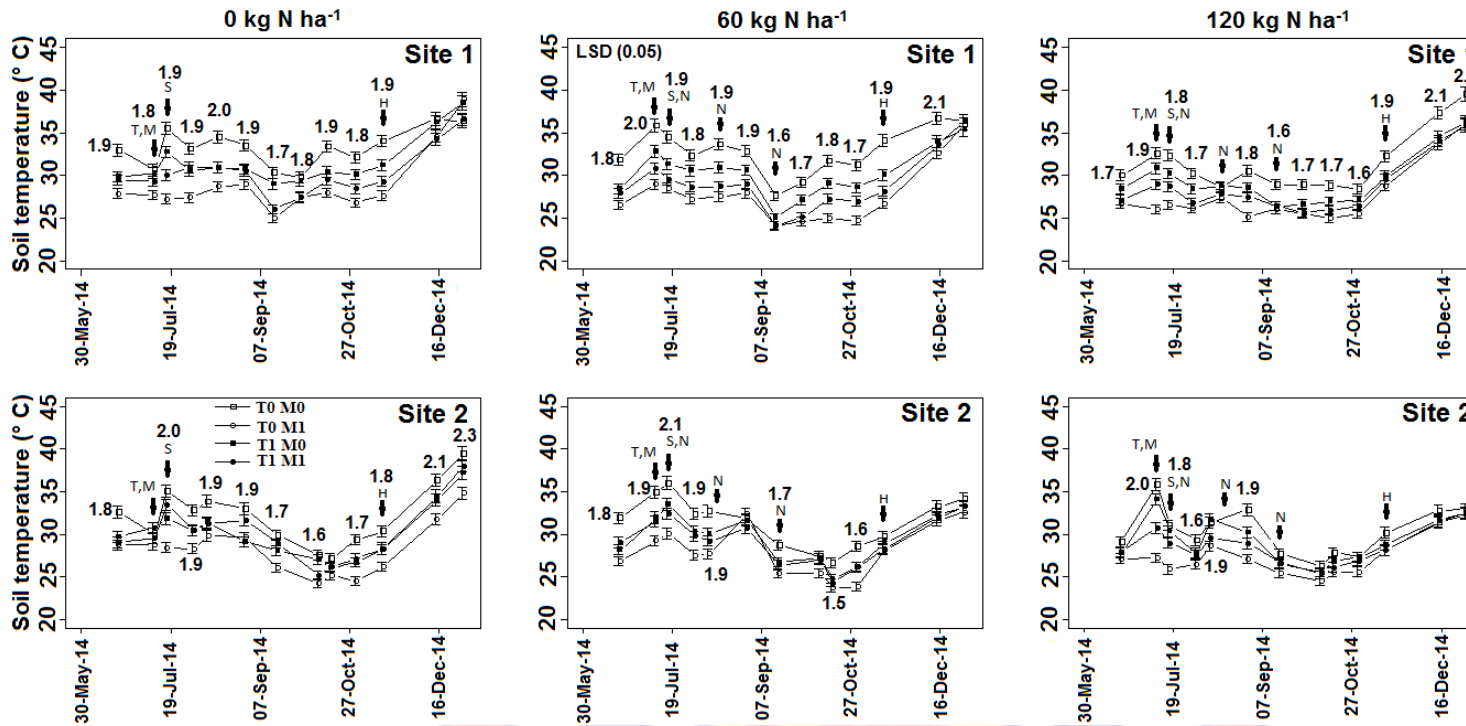


Figure 17: Tillage and rice straw mulch effects on daily soil temperature at different nitrogen fertilization levels during the growing season of 2014 at the experimental Sites 1 and 2.

T: tillage, M: application of rice straw mulch, S: sowing, N: nitrogen fertilizer application, H: harvest. LSD values at specific periods indicate significant differences at $p \leq 0.05$ between treatments; and if no value is shown then the difference is not significant. The error bars represent the standard error.

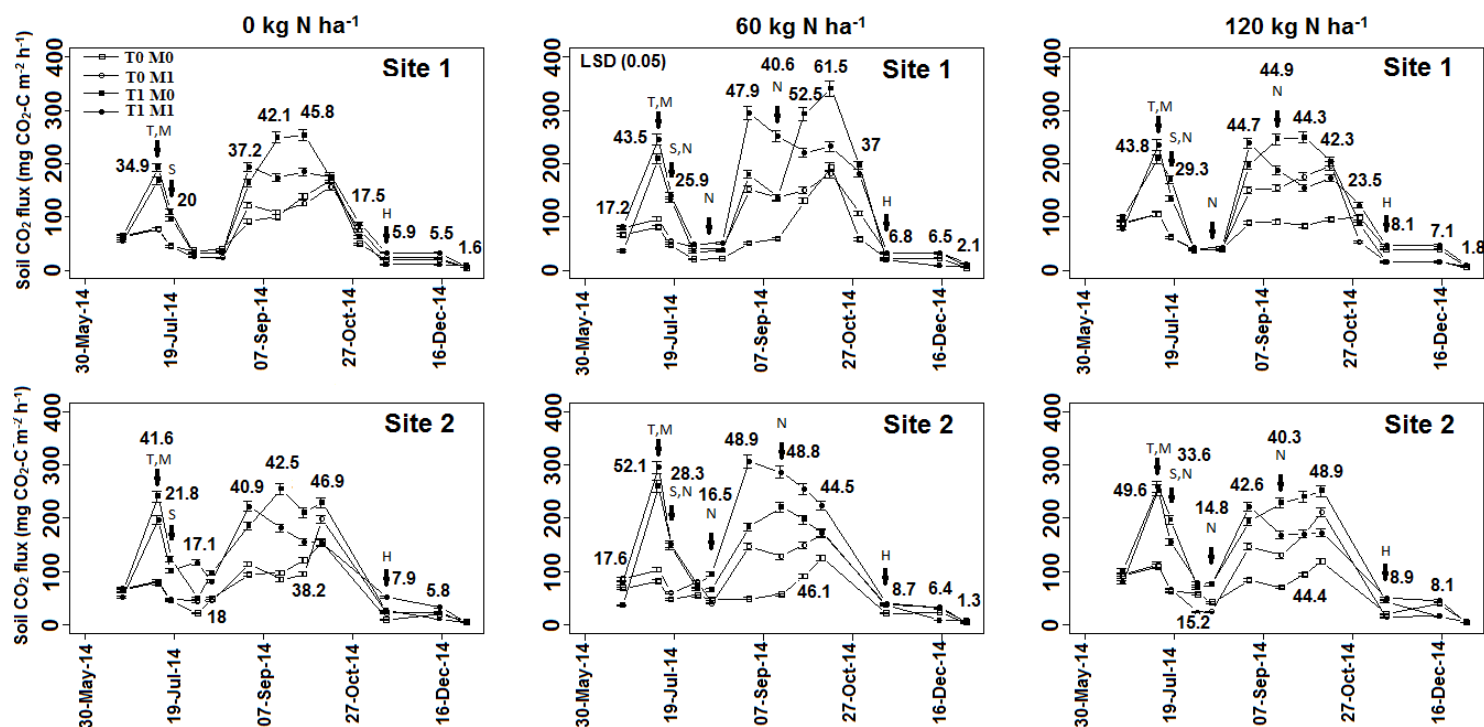


Figure 18: Tillage and rice straw mulch effects on daily soil CO₂ emissions at different nitrogen fertilization levels during the growing season at the experimental Sites 1 and 2.

T: tillage, M: application of rice straw mulch, S: sowing, N: nitrogen fertilizer application, H: harvest. LSD values at specific periods indicate significant differences at $p \leq 0.05$ between treatments; and if no value is shown then the difference is not significant. The error bars represent the standard error.

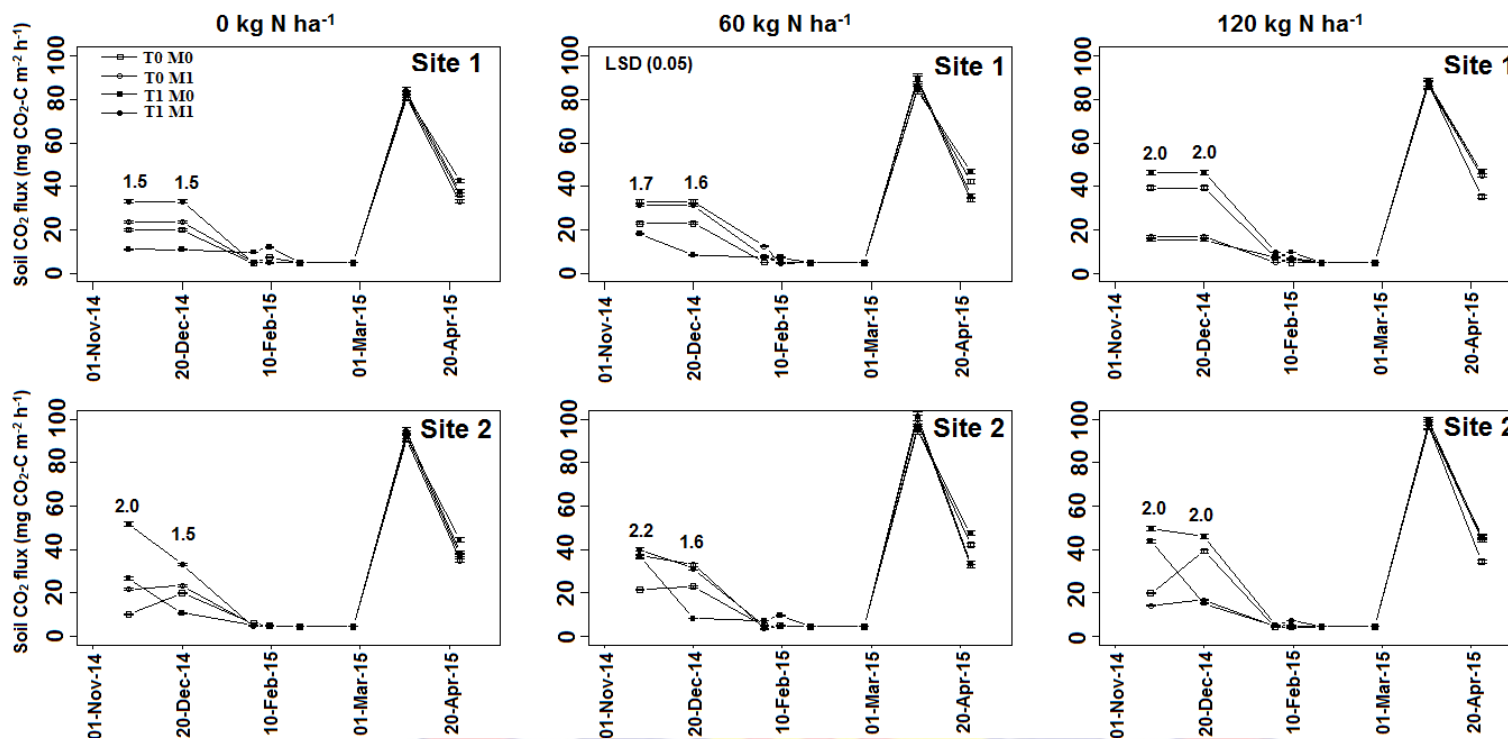


Figure 19: Tillage and rice straw mulch effects on daily soil CO₂ emissions at different nitrogen fertilization levels during the dry season (November 2014-May 2015) at the experimental Sites 1 and 2.

LSD values at specific periods indicate significant differences at $p \leq 0.05$ between treatments; and if no value is shown then the difference is not significant. The error bars represent the standard error.

Table 10-*p*-value for the average soil moisture and soil temperature at 0 – 5 cm depth of the growing season of 2014 (June – November) of the tillage systems, rice straw mulch and nitrogen levels at the two experimental sites

Source of variation	p-value	
	Soil moisture (m ³ m ⁻³)	Soil temperature (°C)
Site (S _i)	<0.01	0.81
Tillage (T)	<0.01	0.70
Rice straw (M)	<0.01	<0.01
Nitrogen (N)	0.87	0.32
S _i x T	<0.01	0.80
S _i x M	0.46	0.18
T x M	0.04	<0.01
S _i x N	0.21	0.87
T x N	0.24	0.98
M x N	0.52	0.68
S _i x T x M	0.19	0.49
T x M x N	0.60	0.44
S _i x M x N	0.69	0.92
S _i x T x M x N	0.01	0.44

Cumulative soil CO₂ emission

Cumulative soil CO₂ emission in the growing season

Cumulative soil CO₂ emission of the growing season (June-October 2014) was higher under manual tillage (5.39 Mg CO₂-C ha⁻¹) than no-tillage (3.14 Mg CO₂-C ha⁻¹) (Table 11). At Site 2, this difference was more pronounced than at Site 1. Application of straw mulch increased cumulative soil CO₂ emission of the growing season by 0.41 Mg CO₂-C ha⁻¹. Across nitrogen fertilizer levels, lower cumulative soil CO₂ emission was recorded under no-till and no straw treatments (2.76 Mg CO₂-C ha⁻¹) and higher under tilled + straw mulch treatments (5.42 Mg CO₂-C ha⁻¹) (Table 12 and Figure 20). Application of nitrogen fertilizer at 60 kg N ha⁻¹ increased cumulative soil CO₂ emission of the growing season by 0.62 Mg CO₂-C ha⁻¹. However, no variation in the cumulative soil CO₂ emission was found between the 60 kg and 120 kg N ha⁻¹ treatments (Table 11).

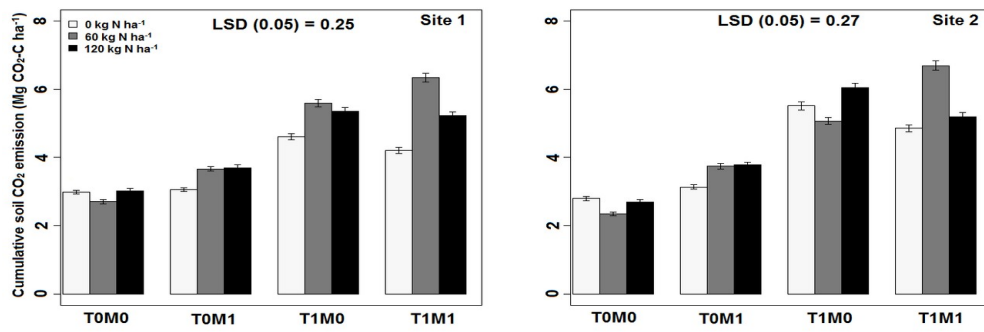


Figure 20: Tillage and rice straw mulch effects on cumulative soil CO₂ emissions by nitrogen fertilization level at the experimental Sites 1 and 2 in the growing season (June-October 2014).

The error bars represent the standard error.

Cumulative soil CO₂ emission during the dry season

Cumulative soil CO₂ emission of the dry season (November 2014-May 2015) was on average 1.09 Mg CO₂-C ha⁻¹ and did not vary significantly with site location, tillage systems, rice straw management and nitrogen levels (Figure 21, Tables 11 and 12).

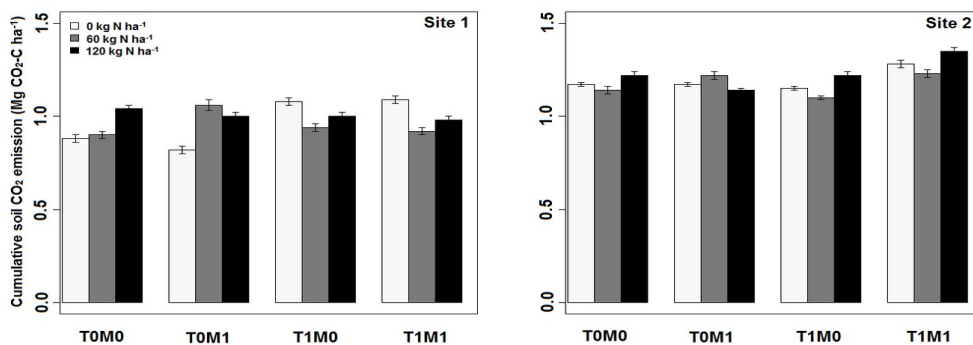


Figure 21: Tillage and rice straw mulch effects on cumulative soil CO₂ emissions by nitrogen fertilization level at the experimental Sites 1 and 2 of the dry season (November 2014 - May 2015).

The error bars represent the standard error.

Cumulative soil CO₂ emission of the year

Cumulative soil CO₂ emission of the year (June 2014-May 2015) varied according to the same pattern as observed during the growing season (Figure 22), except that the main effect of rice straw mulch on cumulative soil CO₂ emission of the year was not significant (Table 11). Cumulative soil CO₂ emission of the year was significantly higher under manual tillage (6.30 Mg CO₂-C ha⁻¹yr⁻¹) than no tillage (4.00 Mg CO₂-C ha⁻¹yr⁻¹) and under nitrogen fertilizer treatments (5.35 Mg CO₂-C ha⁻¹yr⁻¹) compared with zero-nitrogen fertilizer treatments (4.75 Mg CO₂-C ha⁻¹yr⁻¹) (Table 11). On average, cumulative soil CO₂ emission of the growing season represented 83% of the cumulative soil CO₂ emission of the year.

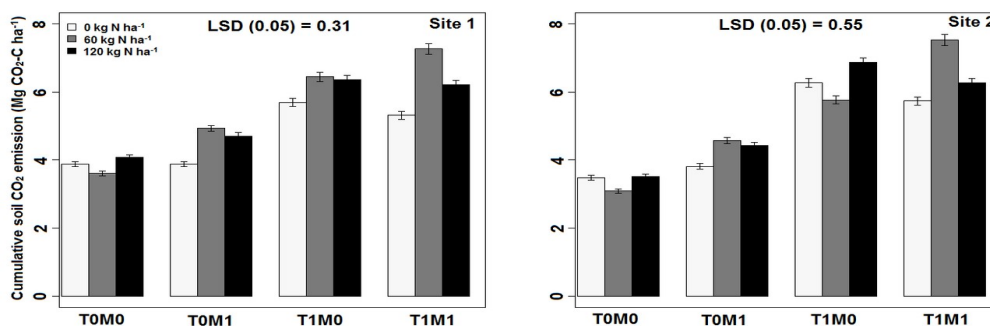


Figure 22: Tillage and rice straw mulch effects on cumulative soil CO₂ emissions of the year (June 2014-May 2015) by nitrogen fertilization level at the experimental Sites 1 and 2.

The error bars represent the standard error.

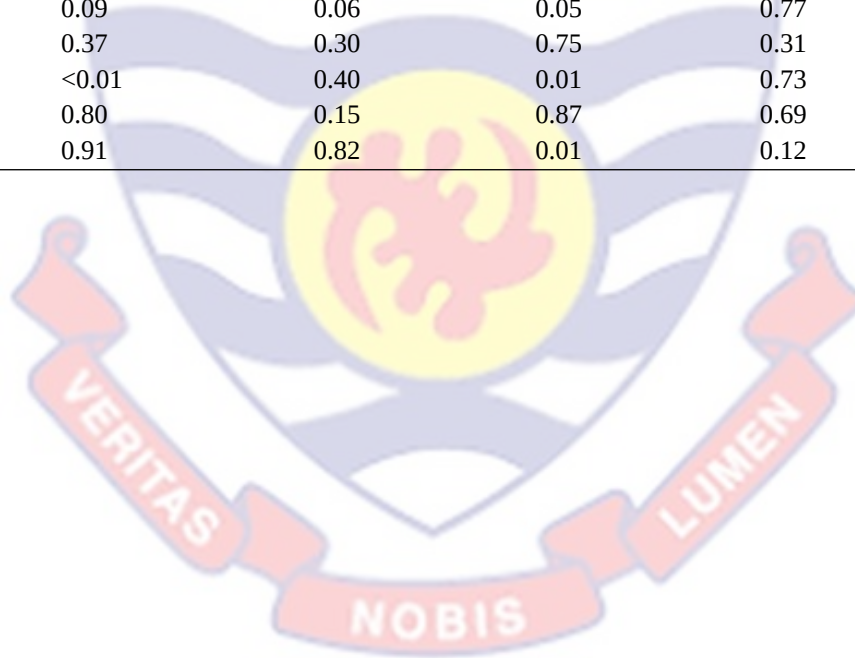
Table 11-Cumulative soil CO₂ emission of the growing season, the dry season, annual and per unit grain yield of the different treatments at the experimental sites

Treatment	Growing season soil CO ₂ (Mg CO ₂ -C ha ⁻¹)	Dry season soil CO ₂ (Mg CO ₂ -C ha ⁻¹)	Annual soil CO ₂ (Mg CO ₂ -C ha ⁻¹)	Soil CO ₂ per yield (Mg C Mg ⁻¹ yield)
Site 1	4.21 a	0.98 a	5.20 a	2.65 a
Site 2	4.32 a	0.78 a	5.11 a	2.07 a
LSD (main site effect)	ns	ns	ns	ns
Tillage systems (T)				
No-tillage (T0)	3.14 a	0.85 a	4.00 a	1.99 a
Manual tillage (T1)	5.39 b	0.91 a	6.30 b	2.72 b
LSD (main T effect)	0.25	ns	0.25	0.57
Straw mulch (M)				
No straw	4.06 a	0.85 a	4.92 a	2.48 a
3 Mg ha ⁻¹ of rice straw	4.47 b	0.91 a	5.38 a	2.28 a
LSD (main M effect)	0.32	ns	ns	ns
Nitrogen levels (N)				
0 kg N ha ⁻¹	3.90 a	0.86 a	4.75 a	4.05 a
60 kg N ha ⁻¹	4.52 b	0.88 a	5.40 b	1.65 b
120 kg N ha ⁻¹	4.38 b	0.92 a	5.30 b	1.38 b
LSD (main N effect)	0.12	ns	0.64	0.41

Numbers followed by different letters in a column within a set are significantly different at $p \leq 0.05$. ns: not significant.

Table 12-p-value of the cumulative soil CO₂ emission for the growing season (Mg CO₂-C ha⁻¹), the dry season (Mg CO₂-C ha⁻¹), annual (Mg CO₂-C ha⁻¹) and per unit grain yield (Mg C Mg⁻¹ yield) of the different treatments at the two experimental sites

Source of variation	p-value			
	Growing season soil CO ₂	Dry season soil CO ₂	Annual soil CO ₂	Soil CO ₂ per yield
Site (S _i)	0.35	0.18	0.47	0.64
Tillage (T)	<0.01	0.08	<0.01	0.01
Rice straw (M)	0.04	0.06	0.08	0.39
Nitrogen (N)	0.04	0.21	0.02	<0.01
S _i x T	0.04	0.08	0.03	0.06
S _i x M	0.76	0.80	0.73	0.99
T x M	0.01	0.28	0.01	0.78
S _i x N	0.76	0.69	0.79	<0.01
T x N	<0.01	0.10	0.03	0.02
M x N	0.09	0.06	0.05	0.77
S _i x T x M	0.37	0.30	0.75	0.31
T x M x N	<0.01	0.40	0.01	0.73
S _i x M x N	0.80	0.15	0.87	0.69
S _i x T x M x N	0.91	0.82	0.01	0.12



Effects of tillage systems, rice straw mulch and inorganic nitrogen application on soil carbon budget

Heterotrophic respiration and root respiration

During the growing season, the heterotrophic respiration (R_h) varied with tillage systems and rice straw mulch (Figures 23 and 24). R_h was higher in manual tillage than no-tillage with the largest difference observed during the day of tillage operation. R_h in rice straw mulch treatments was 8 – 47% higher than R_h in non mulch treatments.

The root respiration (R_r) increased from zero, 7 days after germination at the beginning of rice root development, to a peak value of $185 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ in September, at rice tillering stage, and decreased thereafter until rice harvest (Figures 23 and 24). R_r varied with tillage system, straw mulch and nitrogen fertilizer levels. In general, R_r was much greater in manual tillage compared with no-tillage from mid-August (tillering stage) to early October (flowering stage). There was a slight difference in R_r of manual tillage and no-tillage from flowering stage to harvest. After harvest, R_r ceased. In addition, R_r was higher in nitrogen fertilizer treatments compared with non-nitrogen fertilizer treatments (Figures 23 and 24).

Cumulative carbon loss via heterotrophic respiration

Cumulative carbon loss via heterotrophic respiration (R_h) was significantly affected by tillage systems and rice straw mulch (Table 15). On average, manual tillage had 46% greater cumulative carbon loss via R_h than no-tillage (Table 15). This difference was more pronounced at Site 2 (53%) than at Site 1 (41%) (Tables 13 and 14). Cumulative carbon loss via R_h was

7% greater with rice straw mulch compared with non-straw mulch (Table 15). Nitrogen levels, on the contrary, had no significant effect on the cumulative carbon loss via R_h (Table 15).

Aboveground and belowground carbon

Potential carbon input from aboveground biomass varied with site location, tillage systems and nitrogen levels (Table 15). On average, potential aboveground carbon was $0.33 \text{ Mg C ha}^{-1}$ higher at the lower site (Site 2) than at the upper site (Site 1) (Table 15). Manual tillage increased potential aboveground carbon by $0.27 \text{ Mg C ha}^{-1}$ compared with no-tillage (Table 15). Without nitrogen fertilization, potential aboveground carbon was low at $0.95 \text{ Mg C ha}^{-1}$ and significantly increased by $0.85 \text{ Mg C ha}^{-1}$ and $1.17 \text{ Mg C ha}^{-1}$ with 60 kg N ha^{-1} and 120 kg N ha^{-1} , respectively (Table 15).

Potential carbon input from root biomass, in the top 20 cm soil depth, varied with site location, straw mulch, nitrogen levels (Table 15) and straw and nitrogen levels interaction (Table 16). On average, potential belowground carbon was $0.06 \text{ Mg C ha}^{-1}$ higher at the lower site (Site 2) than at the upper site (Site 1) (Table 15). Though, potential belowground carbon increased with nitrogen levels (Table 15), the increase was higher in straw mulched than in non-mulched treatments (Tables 13 and 14).

Soil carbon budget

Calculations of the soil carbon budget from estimates of potential carbon inputs from aboveground biomass, root biomass, and rice straw mulch minus cumulative carbon loss via heterotrophic respiration resulted in

differences between tillage systems, rice straw mulch and nitrogen levels (Table 15). The lowest soil carbon budget was found under the current farming management practices (manual tillage with no residue and no-nitrogen fertilization) in upland rice fields in northern Benin at $-2.9 \text{ Mg C ha}^{-1}$ (Tables 13 and 14). Mulching of rice straw was the largest determining factor in net soil carbon changes. With 3 Mg ha^{-1} of rice straw mulch, greater changes in soil carbon were observed (-1.9 in no mulch vs. $-0.5 \text{ Mg C ha}^{-1}$ in rice straw mulch treatments) (Table 15). No-tillage treatments had a 1.2 Mg C ha^{-1} higher net carbon change value compared with manual tillage (Table 15). When no nitrogen was applied, soil carbon budget was low ($-1.73 \text{ Mg C ha}^{-1}$) (Table 15) and was independent of tillage systems and rice straw mulch levels (Tables 13 and 14). With no-tillage, 3 Mg ha^{-1} of rice straw mulch and 60 kg N ha^{-1} , soil carbon budget was zero at the upper site (Site 1) and was 0.6 Mg C ha^{-1} at the lower site (Site 2) (Tables 13 and 14). With no other changes in management practices, an increase in nitrogen level from 60 kg N ha^{-1} to 120 kg N ha^{-1} resulted in positive net carbon changes at Site 1 and at Site 2 (Tables 13 and 14). These results point out the importance of using rice straw mulch and nitrogen fertilizer in a no-tillage system for reducing carbon loss via heterotrophic respiration and increasing carbon input in upland rice fields in northern Benin.

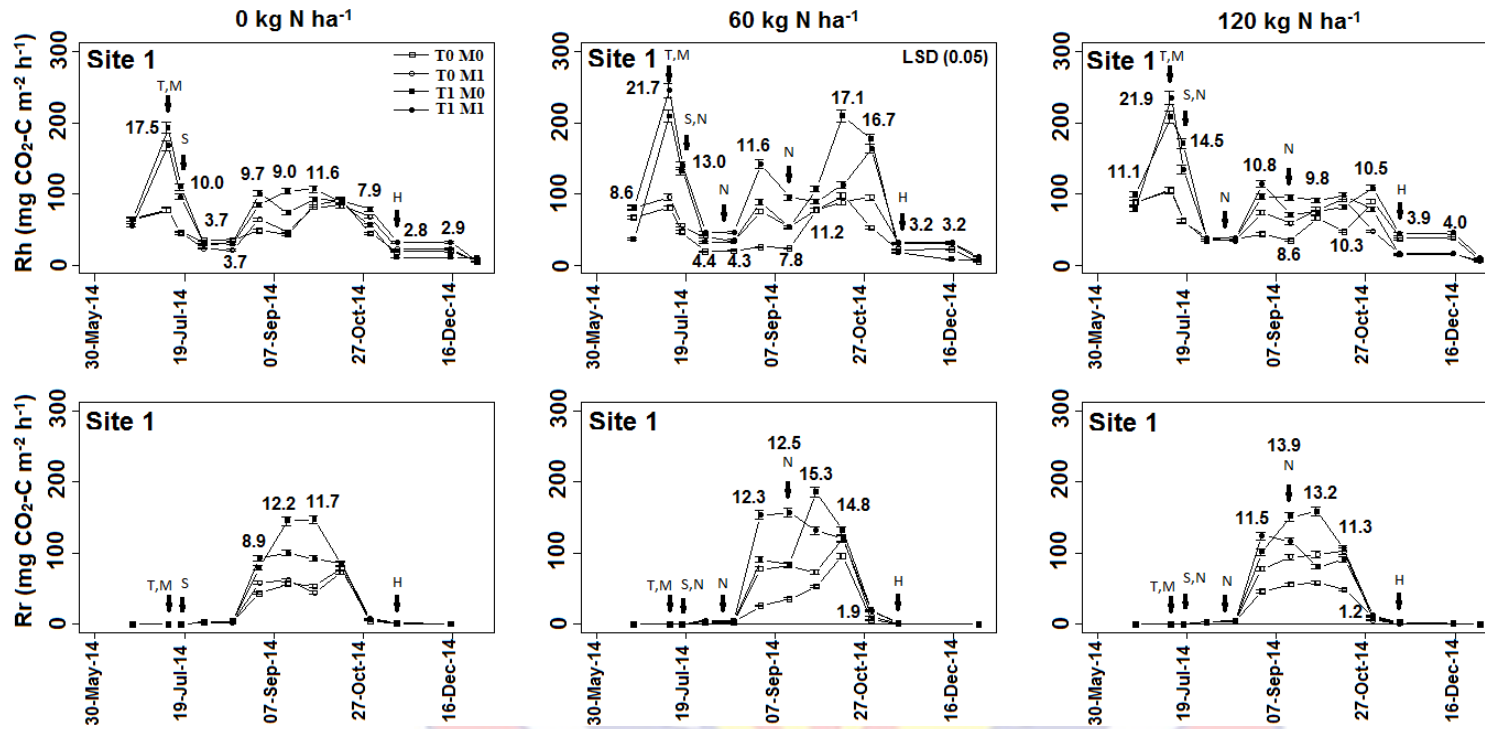


Figure 23: Tillage and rice straw mulch effects on daily heterotrophic respiration (Rh) and root respiration (Rr) at different nitrogen fertilization levels during the growing season at the experimental Site 1.

T: tillage, M: application of rice straw mulch, S: sowing, N: nitrogen fertilizer application, H: harvest. LSD values at specific periods indicate significant differences at $p \leq 0.05$ between treatments; and if no value is shown then the difference is not significant. The error bars represent the standard error.

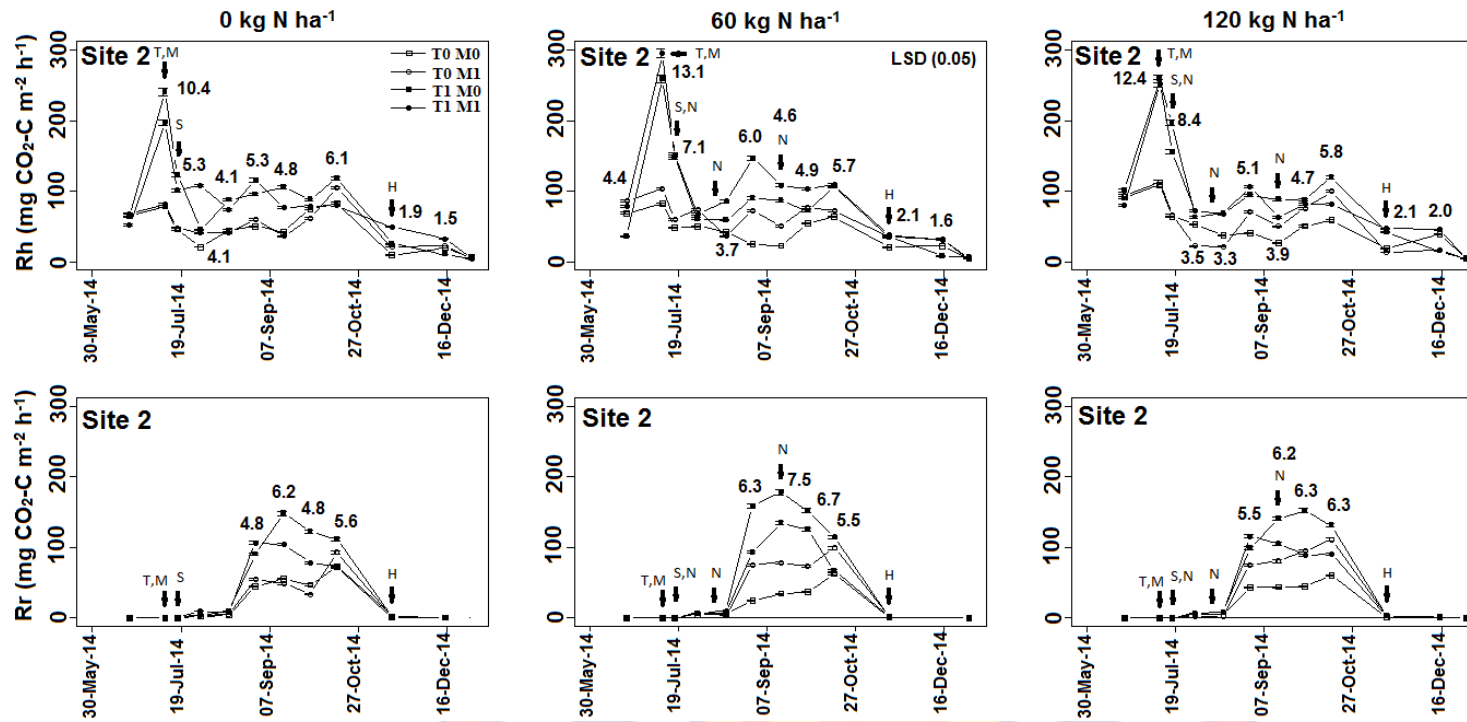


Figure 24: Tillage and rice straw mulch effects on daily heterotrophic respiration (Rh) and root respiration (Rr) at different nitrogen fertilization levels during the growing season at experimental Site 2.

T: tillage, M: application of rice straw mulch, S: sowing, N: nitrogen fertilizer application, H: harvest. LSD values at specific periods indicate significant differences at $p \leq 0.05$ between treatments; and if no value is shown then the difference is not significant. The error bars represent the standard error.

Table 13-Effects of tillage systems, rice straw mulch and nitrogen fertilizer levels on cumulative carbon loss via heterotrophic respiration (CR_h), potential aboveground carbon (PAC), potential belowground carbon (PBC) and soil carbon budget (SCB) at experimental Site 1 from June 2014 to May 2015

Tillage†	Straw mulch (Mg ha ⁻¹)	N fertilization (kg N ha ⁻¹)	CR_h (Mg C ha ⁻¹)	PAC (Mg C ha ⁻¹)	PBC (Mg C ha ⁻¹)	C_{straw} (Mg C ha ⁻¹)	SCB (Mg C ha ⁻¹)
T ₀	0	0	3.0±0.06 f*	0.4±0.01 h	0.1±0.001 d	0	-2.5±0.05 g
T ₀	0	60	2.8±0.05 f	1.4±0.07 e	0.2±0.01 c	0	-1.2±0.05 de
T ₀	0	120	3.2±0.06 e	1.9±0.13 bc	0.3±0.01 b	0	-1.0±0.10 d
T ₀	3	0	2.9±0.06 f	0.6±0.02 gh	0.1±0.04 d	1.6	-0.6±0.04 c
T ₀	3	60	3.5±0.07 d	1.6±0.03 de	0.3±0.01 b	1.6	0±0.06 b
T ₀	3	120	3.3±0.13 e	1.9±0.08 bc	0.4±0.02 a	1.6	+0.6±0.15 a
T ₁	0	0	4.0±0.08 c	0.9±0.14 f	0.2±0.01 c	0	-2.9±0.20 h
T ₁	0	60	4.5±0.09 b	1.7±0.04 cd	0.3±0.01 b	0	-2.5±0.05 g
T ₁	0	120	4.4±0.09 b	2.0±0.07 b	0.4±0.02 a	0	-2.0±0.12 f
T ₁	3	0	3.8±0.08 c	0.7±0.01 fg	0.2±0.006 c	1.6	-1.3±0.06 e
T ₁	3	60	5.1±0.10 a	2.0±0.03 b	0.3±0.01 b	1.6	-1.2±0.07 de
T ₁	3	120	4.6±0.09 b	2.3±0.13 a	0.4±0.02 a	1.6	-0.3±0.20 b
LSD (treatments combination effects)			0.22	0.23	0.03	-	0.30

† Tillage systems are no-tillage (T₀) and manual tillage (T₁).

* Mean values ± standard errors followed by different letters in a column within a set are significantly different at $p \leq 0.05$.

Table 14-Effects of tillage systems, rice straw mulch and nitrogen fertilizer levels on cumulative carbon loss via heterotrophic respiration (CR_h), potential aboveground carbon (PAC), potential belowground carbon (PBC) and soil carbon budget (SCB) at experimental Site 2 from June 2014 to May 2015

Tillage†	Straw mulch (Mg ha ⁻¹)	N fertilization (kg N ha ⁻¹)	CR_h (Mg C ha ⁻¹)	PAC (Mg C ha ⁻¹)	PBC (Mg C ha ⁻¹)	C_{straw} (Mg C ha ⁻¹)	SCB (Mg C ha ⁻¹)
T ₀	0	0	2.9±0.06 hi	1.2±0.08 ef	0.2±0.02 e	0	-1.5±0.09 ef
T ₀	0	60	2.8±0.07 i	1.6±0.05 cde	0.3±0.02 c	0	-0.9±0.11 bcd
T ₀	0	120	3.1±0.06 gh	1.9±0.18 bcd	0.3±0.04 c	0	-0.9±0.18 bc
T ₀	3	0	3.2±0.06 fg	1.0±0.01 f	0.2±0.01 e	1.6	-0.4±0.07 b
T ₀	3	60	3.6±0.07 e	2.1±0.20 b	0.5±0.06 ab	1.6	+0.6±0.31 a
T ₀	3	120	3.3±0.07 f	2.2±0.29 ab	0.5±0.08 a	1.6	+1.0±0.42 a
T ₁	0	0	4.6±0.09 cd	1.5±0.03 def	0.2±0.02 e	0	-2.9±0.11 g
T ₁	0	60	4.5±0.09 d	2.0±0.07 bc	0.3±0.03 cd	0	-2.2±0.16 f
T ₁	0	120	5.1±0.10 b	2.6±0.26 a	0.3±0.09 c	0	-2.2±0.27 ef
T ₁	3	0	4.6±0.09 d	1.2±0.02 ef	0.2±0.01 e	1.6	-1.6±0.09 de
T ₁	3	60	5.4±0.11 a	2.0±0.20 bc	0.4±0.02 c	1.6	-1.4±0.32 cde
T ₁	3	120	4.8±0.10 bc	2.2±0.16 ab	0.4±0.05 bc	1.6	-0.6±0.28 b
LSD (treatments combination effects)			0.24	0.44	0.10	-	0.65

† Tillage systems are no-tillage (T₀) and manual tillage (T₁). * Mean values ± standard errors followed by different letters in a column within a set are significantly different at $p \leq 0.05$ by the least significant difference test.

Table 15-Cumulative carbon loss via heterotrophic respiration (CR_h), potential aboveground carbon (PAC), potential belowground biomass (PBC) and soil carbon budget (SCB) of the tillage systems, rice straw mulch and nitrogen levels from June 2014 to May 2015 at the experimental sites

Treatment	CR_h (Mg C ha ⁻¹)	PAC (Mg C ha ⁻¹)	PBC (Mg C ha ⁻¹)	SCB (Mg C ha ⁻¹)
Site 1	3.77 a	1.46 a	0.25 a	-1.25 a
Site 2	4.00 a	1.79 b	0.31 b	-1.10 a
LSD (main site effect)	ns	0.24	0.05	ns
Tillage systems (T)				
No-tillage (T0)	3.15 a	1.49 a	0.28 a	-0.6 a
Manual tillage (T1)	4.62 b	1.76 b	0.29 a	-1.8 b
LSD (main T effect)	0.15	0.24	ns	0.38
Rice straw (M)				
No straw	3.75 a	1.60 a	0.25 a	-1.90 a
3 Mg ha ⁻¹ of rice straw	4.02 b	1.65 a	0.30 b	-0.50 b
LSD (main M effect)	0.12	ns	0.04	0.34
Nitrogen levels (N)				
0 kg N ha ⁻¹	3.64 a	0.95 a	0.15 a	-1.73 a
60 kg N ha ⁻¹	4.04 a	1.80 b	0.32 b	-1.11 b
120 kg N ha ⁻¹	3.98 a	2.12 c	0.37 c	-0.69 b
LSD (main N effect)	ns	0.17	0.04	0.51

Numbers followed by different letters in a column within a set are significantly different at $p \leq 0.05$. ns: not significant.

Table 16-p-value for cumulative carbon loss via heterotrophic respiration (CR_h), potential aboveground carbon (PAC), potential belowground biomass (PBC) and soil carbon budget (SCB) of the tillage systems, rice straw mulch and nitrogen levels from June 2014 to May 2015 at the two experimental sites

Source of variation	p-value			
	CR _h (Mg C ha ⁻¹)	PAC (Mg C ha ⁻¹)	PBC (Mg C ha ⁻¹)	SCB (Mg C ha ⁻¹)
Site (Si)	0.14	0.01	0.02	0.43
Tillage (T)	<0.01	0.02	0.69	<0.01
Rice straw (M)	0.03	0.36	0.01	<0.01
Nitrogen (N)	0.15	<0.01	<0.01	<0.01
Si x T	0.01	0.82	0.08	0.16
Si x M	0.84	0.59	0.37	0.64
T x M	0.38	0.31	0.22	0.45
Si x N	0.79	0.13	0.44	0.88
T x N	0.13	0.95	0.17	0.43
M x N	0.15	0.13	0.01	0.48
Si x T x M	0.54	0.37	0.78	0.54
T x M x N	0.85	0.97	0.62	0.82
Si x M x N	0.93	0.64	0.54	0.93
Si x T x M x N	0.02	0.06	0.64	0.11

Factors controlling soil CO₂ emission

Responses of soil CO₂ emission to soil temperature and soil moisture

At a daily scale, during the growing and the dry seasons, no clear relationship was observed between soil CO₂ emission and soil temperature (Figure 25), but a highly significant correlation was found with soil moisture during the growing season ($r = 0.95$, $p < 0.01$) (Figure 26). This suggests that soil moisture was the main factor explaining the seasonal variability of soil CO₂ emission at the two sites.

Factors affecting root respiration and heterotrophic respiration

Using stepwise regression analysis, day after sowing (DAS), soil CO₂ emission (F), and soil moisture (θ_v) were positive drivers for percentage of root respiration (R_r) contribution to soil CO₂ emission (Table 17). This indicates that the contribution of R_r , relative to R_h , to F was positively affected by increasing root growth with increasing time after sowing, and that high soil

CO₂ emission values during the growing season were due to greater contribution from R_r, especially in wet days.

The heterotrophic respiration was activated by soil moisture availability but showed low variation with increasing soil moisture during the growing season (Figure 27). Thus, the large soil CO₂ emission observed during the growing season was due to the availability of soil moisture that permits the microbial activity and higher root respiration as a consequence of crop growth.

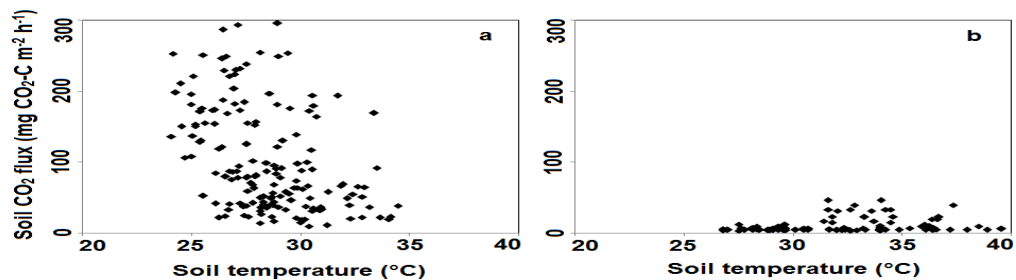


Figure 25: Relationship between daily soil CO₂ emission and soil temperature during (a) the growing season (June 2014–October 2014) and (b) the dry season (November 2014–May 2015).

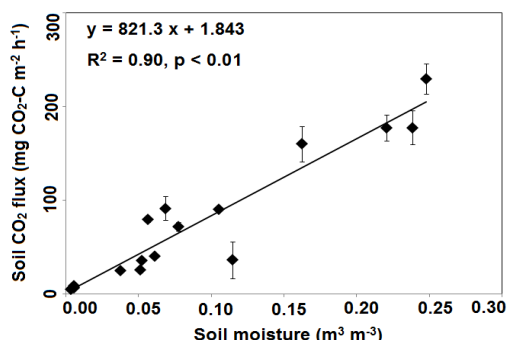


Figure 26: Relationship between daily soil CO₂ emission and soil moisture during the growing season (June 2014-October 2014).

Each point is a mean of 24 data points. Error bars represent the standard error.

Table 17-*Contribution of root respiration (R_r) to soil CO₂ during the growing season (June 2014-October 2014) as affected by days after sowing (DAS), soil moisture (θ_v) (m³ m⁻³) and soil CO₂ emission (F) (mg CO₂-C m⁻² h⁻¹)*

	Estimate	p
Intercept	-17.8	<0.01
DAS	+0.17	<0.01
θ _v	+183	<0.01
F	+0.0836	<0.01
Summary of statistics		
p	<0.01	
R ²	0.81	
Observations	155	
Regression model	-17.8+0.17DAS+183θ _v +0.0836F	

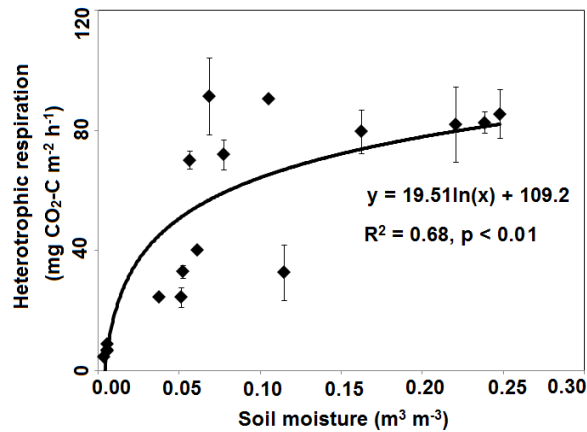


Figure 27: Relationship between daily heterotrophic respiration and soil moisture during the growing season (June 2014–October 2014). Each point is a mean of 24 data points. Error bars represent the standard error.

Appropriate combination of tillage systems, rice straw mulch and nitrogen fertilization to reduce soil CO₂ emission and increase soil carbon budget and upland rice yield in northern Benin

Grain yield of rice

In order to study the annual variability of rice yields under the different treatments, it appeared useful to first describe the rainfall distribution during the growing seasons. During the vegetative stage of rice plants (from sowing to panicle initiation), the rainfall values were 433, 323 and 392 mm in 2013, 2014 and 2015, respectively (Figure 28). During the reproductive stage (from panicle initiation to flowering), the rainfall values were 110, 288 and 167 mm in 2013, 2014 and 2015, respectively. During the ripening stage (from flowering to grain maturity), the rainfall values were 0, 8 and 97 mm in 2013,

2014 and 2015, respectively. Overall, during the growing seasons, the total rainfall values were 544, 619 and 656 mm in 2013, 2014 and 2015, respectively.

The grain yield of rice significantly varied with year of experiment, site location, rice straw mulch and nitrogen levels (Table 18). At the upper site (Site 1), average grain yields of rice were in the order of yield in 2013 (1.62 Mg ha^{-1}) < yield in 2014 (2.66 Mg ha^{-1}) < yield in 2015 (2.85 Mg ha^{-1}). At the lower site (Site 2), average grain yield was lower in 2014 than in 2015. In addition, average yields were lower at the upper site (Site 1) than at the lower site (Site 2) in 2014 and 2015 (Table 18).

There was a significant rice straw mulch effect on grain yield of rice (Table 18). Average grain yields of rice were significantly higher in rice straw mulch treatments compared with non-mulch treatments. Grain yields of rice significantly increased with increase in nitrogen levels (Table 18). Increases in yield were 1.9 Mg ha^{-1} and 2.5 Mg ha^{-1} at Site 1 and Site 2, respectively, when 60 kg N ha^{-1} and when no nitrogen was applied. Increase in nitrogen level from 60 kg N ha^{-1} to 120 kg N ha^{-1} enhanced rice grain yield by 1.0 Mg ha^{-1} and 0.3 Mg ha^{-1} at Site 1 and Site 2, respectively.

There was a significant interaction effect of rice straw mulch and nitrogen fertilization on grain yield of rice (Table 19). At both sites and for the two tillage systems, grain yields of rice were higher under rice straw mulch and nitrogen fertilization compared with the yields under rice straw mulch alone or nitrogen fertilization alone (Table 20).

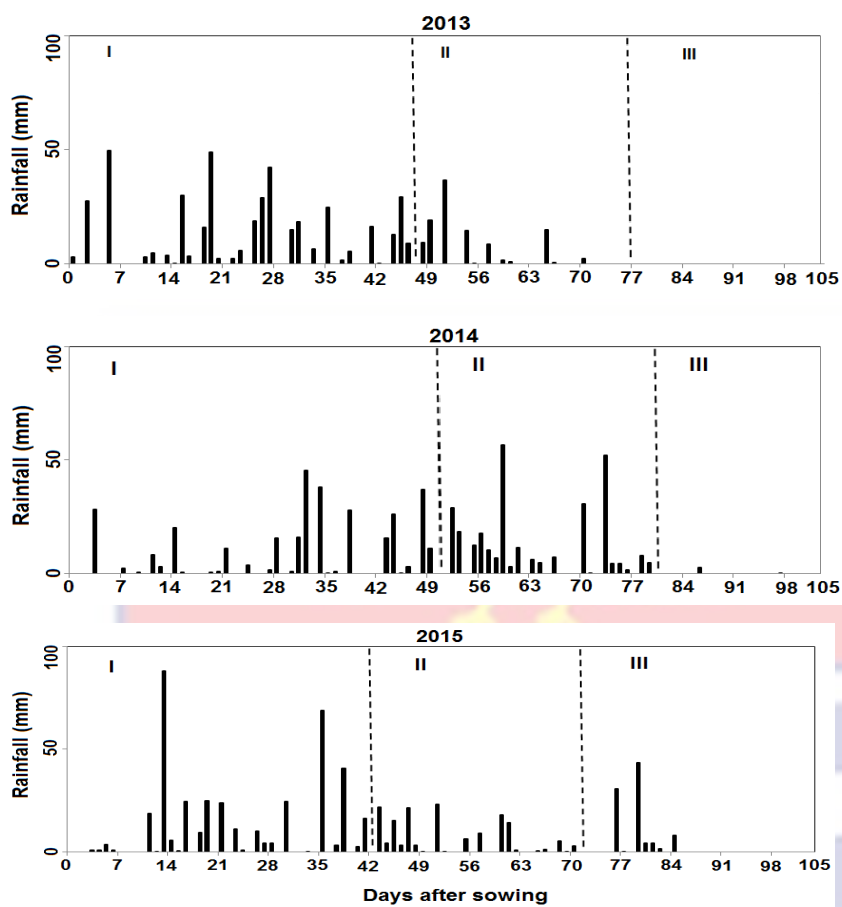


Figure 28: Rainfall distribution during (I) the vegetative stage, (II) the reproductive stage and (III) the ripening stage of rice plants during three growing seasons (2013, 2014 and 2015).

Agronomic efficiency of nitrogen

The agronomic efficiency of nitrogen varied with nitrogen levels (Table 21) and straw mulch and nitrogen levels interaction (Table 19). The increase in nitrogen from 60 kg N ha⁻¹ to 120 kg N ha⁻¹ decreased the AEN (Table 21). The combination of straw mulch and 60 kg N ha⁻¹ achieved significantly higher agronomic efficiency of nitrogen at the two tillage systems (Table 22). Results showed that combination of rice straw mulch and 60 kg N ha⁻¹ can give rice yield equivalent to that of no straw and 120 kg N ha⁻¹ across tillage systems (Table 22).

Cumulative soil CO₂ emission per unit grain yield

There was a significant tillage and nitrogen interaction effect on soil CO₂ emission per unit grain yield (Table 12). Higher amount of soil CO₂ emission per unit grain yield (4.36 – 4.83) was obtained under manual tillage, and no nitrogen application. On the contrary, lower soil CO₂ emission per grain yield (1.04 – 1.27) was obtained at the two sites by combining no-tillage and 60 or 120 kg N ha⁻¹ (Figure 29). No significant effect of rice straw mulch on soil CO₂ emission per unit grain yield was found (Table 11).

These results indicate that the current practices of manual tillage, with no residue and no nitrogen fertilization in upland rice fields lead to higher amount of soil CO₂ emission per unit grain yield and lower soil carbon budget and rice yield. On the contrary, no-tillage and rice straw mulch and 60 kg N ha⁻¹ reduced soil CO₂ emission per unit grain yield and increased both soil carbon budget and rice yield response to nitrogen fertilization.

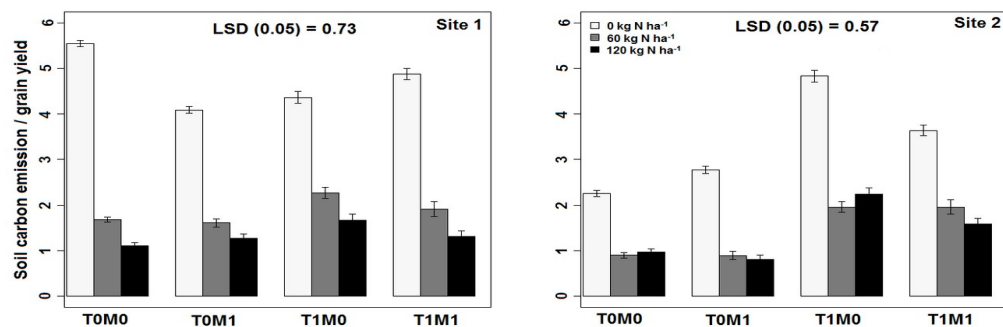


Figure 29: Tillage and rice straw mulch effects on the amount of soil CO₂ emission per unit grain yield at different nitrogen fertilizer levels at the experimental Sites 1 and 2 from June 2014 to May 2015. Error bars represent the standard error.

Table 18-Grain yield of rice for the growing seasons at the experimental Sites 1 and 2 of the different treatments

Treatment	Grain yield (Mg ha ⁻¹)				
	Site 1			Site 2	
	2013	2014	2015	2014	2015
Tillage systems (T)					
No-tillage (T ₀)	1.60 a	2.40 a	2.65 a	3.50 a	3.77 a
Manual tillage (T ₁)	1.64 a	2.93 a	3.06 a	2.90 a	3.03 a
LSD (main T effect)	ns	ns	ns	ns	ns
Rice straw (M)					
No straw	1.35 a	2.46 a	2.49 a	2.71 a	2.81 a
3 Mg ha ⁻¹ of rice straw	1.89 b	2.86 b	3.22 b	3.77 b	3.99 b
LSD (main M effect)	0.44	0.27	0.30	0.96	1.12
Nitrogen levels (N)					
0 kg N ha ⁻¹	0.69 a	1.04 a	1.16 a	1.47 a	1.63 a
60 kg N ha ⁻¹	1.76 b	2.97 b	3.20 b	4.01 b	4.12 b
120 kg N ha ⁻¹	2.42 c	3.97 c	4.20 c	4.25 b	4.45 b
LSD (main N effect)	0.26	0.37	0.43	0.85	1.12

Numbers followed by different letters in a column within a set are significantly different at $p \leq 0.05$. ns: not significant.

Table 19-p-value for grain yield of rice ($Mg\ ha^{-1}$) and agronomic efficiency of nitrogen ($kg\ kg^{-1}$) of the different treatments during the growing seasons at the experimental Sites 1 and 2

Source of variation	p-value for grain yield					p-value for agronomic efficiency of nitrogen				
	Site 1			Site 2		Site 1			Site 2	
	2013	2014	2015	2014	2015	2013	2014	2015	2014	2015
Tillage (T)	0.86	0.17	0.32	0.15	0.18	0.90	0.35	0.62	0.07	0.24
Rice straw (M)	0.02	0.03	0.04	0.03	0.04	0.57	0.15	0.08	0.04	0.06
Nitrogen (N)	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	0.01	0.01	0.01	0.02
T x M	0.81	0.94	0.85	0.61	0.94	0.74	0.22	0.28	0.16	0.30
T x N	0.69	0.64	0.96	0.39	0.53	0.35	0.45	0.80	0.82	0.85
M x N	0.04	0.01	0.01	0.05	0.02	0.04	0.01	<0.01	0.02	0.04
M x T	0.81	0.94	0.85	0.61	0.94	0.74	0.30	0.28	0.16	0.30
T x M x N	0.36	0.42	0.57	0.40	0.72	0.22	0.99	0.92	0.87	0.92

Table 20-Effects of tillage systems, rice straw mulch and nitrogen fertilizer levels on grain yield of rice during the growing seasons at the experimental Sites 1 and 2

Tillage ^f	Mulch (Mg ha ⁻¹)	N levels (kg N ha ⁻¹)	Grain yield of rice (Mg ha ⁻¹)				
			Site 1			Site 2	
			2013	2014	2015	2014	2015
T ₀	0	0	0.5±0.1 f*	0.7±0.1 f	0.8±0.1 f	1.6±0.3 de	1.8±0.2 de
T ₀	0	60	1.7±0.1 cd	2.2±0.1 d	2.3±0.2 d	3.5±0.2 c	3.5±0.3 bcd
T ₀	0	120	1.9±0.1 bc	3.8±0.2 b	3.6±0.2 c	3.7±0.4 c	4.1±0.2 bc
T ₀	3	0	0.8±0.1 e	0.9±0.1 f	1.5±0.1 ef	1.4±0.1 e	1.6±0.2 de
T ₀	3	60	1.9±0.1 bc	3.1±0.1 c	3.6±0.2 c	5.4±0.7 ab	5.3±0.5 ab
T ₀	3	120	2.7±0.2 a	3.7±0.1 b	4.4±0.3 ab	6.0±1.1 a	6.2±0.6 a
T ₁	0	0	0.5±0.1 f	1.4±0.2 e	1.4±0.1 e	1.3±0.1 e	1.3±0.1 e
T ₁	0	60	1.4±0.1 d	2.8±0.1 c	2.9±0.2 d	3.0±0.1 cd	3.0±0.3 cde
T ₁	0	120	2.1±0.1 b	3.9±0.2 b	4.0±0.2 bc	3.2±0.4 c	3.1±0.4 cde
T ₁	3	0	0.9±0.1 e	1.1±0.1 ef	1.3±0.2 ef	1.6±0.1 e	1.8±0.4 de
T ₁	3	60	2.0±0.1 b	3.8±0.1 b	4.0±0.2 bc	4.2±0.6 bc	4.6±0.4 abc
T ₁	3	120	2.8±0.2 a	4.5±0.3 a	4.8±0.3 a	4.1±0.4 bc	4.4±0.5 abc
LSD (treatments combination effect)			0.3	0.5	0.6	1.4	2.1

^f Tillage systems are no-tillage (T₀) and manual tillage (T₁).

* Mean values ± standard errors followed by different letters in a column within a set are significantly different at $p \leq 0.05$.

Table 21-Agronomic efficiency of nitrogen during the growing seasons at the experimental Sites 1 and 2 of the different treatments

Treatment	Agronomic efficiency of nitrogen (kg kg ⁻¹)				
	Site 1			Site 2	
	2013	2014	2015	2014	2015
Tillage systems (T)					
No-tillage (T ₀)	10.96 a	18.06 a	19.42 a	25.54 a	24.68 a
Manual tillage (T ₁)	10.39 a	19.60 a	20.23 a	18.21 a	18.76 a
LSD (main T effect)	ns	ns	ns	ns	ns
Rice straw (M)					
No straw	9.99 a	15.59 a	15.72 a	15.37 a	15.22 a
3 Mg ha ⁻¹ of rice straw	11.36 a	22.08 a	23.93 a	28.38 b	28.23 a
LSD (main M effect)	ns	ns	ns	12.69	ns
Nitrogen levels (N)					
0 kg N ha ⁻¹	-	-	-	-	-
60 kg N ha ⁻¹	17.71 a	32.09 a	34.11 a	42.42 a	41.62 a
120 kg N ha ⁻¹	14.33 b	24.40 b	25.36 b	23.21 b	23.55 b
LSD (main N effect)	1.46	4.61	4.72	10.37	12.44

Numbers followed by different letters in a column within a set are significantly different at $p \leq 0.05$. ns: not significant.

Table 22-Effects of tillage systems, rice straw mulch and nitrogen fertilizer levels on the agronomic efficiency of nitrogen during the growing seasons at the experimental Sites 1 and 2

Tillage ^f	Mulch (Mg ha ⁻¹)	N levels (kg N ha ⁻¹)	Agronomic efficiency of nitrogen (kg kg ⁻¹)				
			Site 1			Site 2	
			2013	2014	2015	2014	2015
T ₀	0	0	-	-	-	-	-
T ₀	0	60	19±0.1 a*	24±1.5 cd	25±2.0 bc	31±1.8 bcd	28±5.5 bc
T ₀	0	120	12±0.8 d	25±1.9 cd	23±1.4 c	18±3.7 d	18±5.7 bc
T ₀	3	0	-	-	-	-	-
T ₀	3	60	18±1.1 ab	36±1.5 b	41±2.5 a	66±1.9 a	62±2.9 a
T ₀	3	120	16±1.0 bc	23±1.0 cd	27±1.8 bc	38±1.6 bc	39±2.4 abc
T ₁	0	0	-	-	-	-	-
T ₁	0	60	15±0.9 cd	23±4.6 cd	24±1.5 bc	27±2.2 bcd	29±4.9 bc
T ₁	0	120	13±0.8 cd	20±0.8 d	21±1.3 c	15±3.1 d	15±4.5 c
T ₁	3	0	-	-	-	-	-
T ₁	3	60	18±1.1 ab	45±0.8 a	46±2.6 a	44±1.8 b	46±1.9 ab
T ₁	3	120	16±1.0 bc	29±2.6 c	30±1.8 b	21±3.6 cd	21±3.8 bc
LSD (treatments combination effect)			2.6	6.4	5.6	20.2	28.6

^f Tillage systems are no-tillage (T₀) and manual tillage (T₁).

* Mean values ± standard errors followed by different letters in a column within a set are significantly different at p ≤ 0.05.

CHAPTER FIVE: DISCUSSION

Soil CO₂ emission

Across tillage systems, rice straw mulch and nitrogen levels, the mean rate of soil CO₂ emission at the upper site was 91.95 mg CO₂-C h⁻¹ m⁻². At the lower site, the mean rate of soil CO₂ emission was 95.73 mg CO₂-C h⁻¹ m⁻². Mean rates of soil CO₂ emission observed in this study were within the range (54.54 – 242.72 mg CO₂-C h⁻¹ m⁻²) of a previous study in agricultural ecosystems in northern Benin by Mulindabigwi (2005). Higher cumulative soil CO₂ emissions of the growing season were observed in manual tillage (5.39 Mg CO₂-C ha⁻¹) than in no-tillage (3.14 Mg CO₂-C ha⁻¹) (Table 11). This could be attributed to mineralization of soil organic matter due to increase in soil aeration (Al-Kaisi & Yin, 2005).

The CO₂ flux of as much as 250 mg CO₂-C h⁻¹ m⁻² following tillage operation observed in this study is close to 214 mg CO₂-C h⁻¹ m⁻² found within the first two hours after tillage on fine loamy soil in Ames in the United States by Al-Kaisi and Yin (2005). Tillage can result in an immediate short-term outburst of CO₂ due to decrease in partial pressure of CO₂ in soil air, followed by disturbance of soil aggregates and pores, and sudden release of CO₂ from the soil solution (Rochette & Angers, 1999). Soil CO₂ emissions were low two weeks after tillage regardless of farming management practices (Figure 18), suggesting that the effect of tillage on CO₂ flux was short-lived, as found by Sainju, Jabro, and Stevens (2006) in western North Dakota, United States, on a Lihen sandy loamy soil.

Soil carbon emission data showed that the application of rice straw mulch caused an increase in soil CO₂ emissions compared with the non-mulched treatments during the growing season (Table 11). Cumulative soil CO₂ emissions of the growing season were 0.41 Mg CO₂-C ha⁻¹ higher in mulched treatments compared with non-mulched treatments (4.06 in no mulch vs. 4.47 Mg CO₂-C ha⁻¹ in mulch). Higher soil carbon emissions in mulched treatments compared with non-mulched treatments were also found by Bhattacharyya et al. (2012) and Heller et al. (2007). This might be due to higher microbial activity in mulched treatments and the conversion of rice straw carbon to soil organic carbon (Khalil, Hossain, & Schmidhalter, 2005).

Very few studies regarding the effects of farming management practices on soil CO₂ emissions have previously been reported in West Africa (Lamade et al., 1996; Mulindabigwi, 2005). It is expected that the application of inorganic N fertilizers along with organic materials will affect the mineralization of soil organic matter and crop productions, which will ultimately affect soil CO₂ emissions (Lamade et al., 1996). However, reported variations in soil CO₂ emissions following fertilizer applications have not been consistent so far. While Al-Kaisi et al. (2008) reported that fertilizer application suppresses CO₂ emissions, Mulvaney et al. (2009), on the other hand, have reported that it enhances CO₂ emissions. Moreover, some other scientists such as Lee, Doolittle, and Owens (2007) reported that fertilizer application has no effect on soil CO₂ emissions. This study however, showed that the use of 60 kg N ha⁻¹ enhanced CO₂ emissions compared with the no-N fertilizer treatment, but that further increases in N did not increase soil CO₂

emissions (Table 11). Moreover, the use of different levels of N fertilizer relative to the non-fertilized level significantly increased carbon input from aboveground and belowground biomass (Tables 13 and 14). This result suggests that the higher soil CO₂ emission fluxes associated with nitrogen fertilization use might be due to greater availability of the carbon substrates resulting in higher microbial activity as reported by Fisk and Fahey (2001) or increased root growth and greater root respiration as reported by Lamade et al. (1996).

Soil carbon budget

Across tillage systems, rice straw mulch and nitrogen level, average contribution of root respiration to soil CO₂ emission during the growing season was 25%. This value falls within the range of 10 to 45% reported in annual croplands (Raich & Mora, 2005; Rochette et al., 1999). Root respiration and heterotrophic respiration peaks coincided with some exceptions (Figures 23 and 24). This could be attributed to the fact that root respiration is coupled with photosynthesis rates, which are influenced by environmental conditions such as soil moisture, and farming management practices similar to heterotrophic respiration in Benin (Ago et al., 2014; Ago, Serça, Agbossou, Galle, & Aubinet, 2015; Lamade et al., 1996; Mulindabigwi, 2005).

Cumulative carbon loss via heterotrophic respiration was 46% greater in manual tillage than no-tillage (Tables 13 and 14). Disturbance of soil aggregates and pores, and sudden release of CO₂ from the soil solution due to

tillage operation may be a major reason for having greater cumulative carbon loss via heterotrophic respiration under manual tillage compared with no-tillage (Rochette & Angers, 1999). On average, tillage operation increased heterotrophic respiration by $119 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ the day of tillage (Figure 24). Similar results were reported by Al-Kaisi and Yin (2005) on fine loamy soil in Ames, United States.

Cumulative carbon loss via heterotrophic respiration was 7% greater with rice straw mulch compared with non-straw mulch (Tables 13 and 14). This may be attributed to higher availability of carbon substrate for mineralization due to rice straw mulch which may increase the soil microbial activity (Fisk & Fahey, 2001).

Across tillage types, rice straw mulch and nitrogen levels, average potential carbon inputs from aboveground and root biomass were 1.5 Mg C ha^{-1} and 0.3 Mg C ha^{-1} , respectively (Tables 13 and 14). These values fall within the range of 1.2 to 3.0 Mg C ha^{-1} and 0.3 to 0.7 Mg C ha^{-1} reported by Mulindabigwi (2005) respectively for aboveground carbon and root biomass carbon in rice fields in northern Benin. Guzman and Al-Kaisi (2014) also reported an increase in potential carbon input from aboveground biomass and root biomass with nitrogen fertilizer addition on clay loamy and silty clay loamy soils in Iowa, United States. This increase in carbon input from plant biomass with nitrogen fertilizer addition can be attributed to increases in aboveground and root biomass.

Under the current management practices (manual tillage, with no residue and no nitrogen fertilization) in upland rice fields in northern Benin,

the carbon added as aboveground biomass and root biomass was not enough to compensate for the loss of carbon from organic matter decomposition rendering upland rice fields as net sources of atmospheric CO₂. Ago, Agbossou, Ozer, and Aubinet (2016) reported that under similar farming management practices, agricultural fields in northern Benin were net sources of atmospheric CO₂. Conversion of manual tillage to no-tillage significantly reduced cumulative carbon loss via heterotrophic respiration. Rice straw mulching and nitrogen fertilization increased carbon input. As consequence, no-tillage with rice straw mulch and nitrogen fertilization resulted in higher soil carbon budgets at both experimental sites.

Factors controlling soil CO₂ emission

Soil carbon emission which is mainly dependent on autotrophic (root) and heterotrophic (microbial) activities is mainly controlled by soil moisture at our studied sites (Figure 26) as reported by other authors for similar ecosystems in Benin (Ago et al., 2014; Lamade et al., 1996; Mulindabigwi, 2005). Contrary to the results of Brümmer et al. (2008), our studies revealed no relationship between soil CO₂ flux and soil temperature (Figure 25). This could be attributed to the fact that the temperature variability at our investigated sites is relatively low. Mulindabigwi (2005) also reported no significant effect of soil temperature on soil CO₂ flux in northern Benin due to only slight variation of soil temperature and concluded that soil CO₂ flux was mainly dependent on soil moisture.

There was an immediate increase in heterotrophic respiration after the first rain events following drought periods (Figure 19). This was clearly observed in April 2015 with 93 mm cumulated rainfall. When no rain was recorded during a long period, a decrease of heterotrophic respiration was observed. Reversely, when rainfall events became more regular, the heterotrophic respiration increased continuously before reaching its highest values ($80 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$) and then showed low dependency with increasing soil moisture (Figure 27). After the last rain, the heterotrophic respiration tended to decrease back to low values at the end of rainy season and during the subsequent dry season. During drought periods, the soil micro-organisms activity may be very low and the soil wetted by first rains may induce bursts in the activity of soil micro-organisms. This sudden increase in the heterotrophic respiration following rainfall after a long drought period was also reported by Boulain et al. (2009) in millet fields in Niger.

During the rainy season when soil moisture was sufficient to permit a substantial activity of the microbial population, variation in soil CO_2 emission was driven by root respiration associated with crop growth (Table 17). Therefore, it would be possible to estimate soil CO_2 emission in the growing season with root respiratory flux from root biomass. In southern Benin, Lamade et al. (1996) found in an oil palm field an exponential relationship between root respiration and root density while the heterotrophic respiration showed low dependency with soil moisture.

Grain yield and soil CO₂ emission per unit grain yield

Averaged over growing seasons, tillage systems, rice straw mulch and nitrogen levels, mean rice yields were 2.76 Mg ha⁻¹ and 3.32 Mg ha⁻¹ at the upper site and at the lower site, respectively (Table 20). Mean rice yields observed in this study were within the range (1.56 – 3.40 Mg ha⁻¹) of mean upland rice cultivars yields in West Africa (Saito & Futakuchi, 2009). Differences in grain yields across years and sites can be explained by rainfall data and soil properties. Lower average grain yields were found in 2013 than in 2014 and in 2015 possibly due to the lower cumulative rainfall recorded during the growing season of 2013 (547 mm) compared with those of 2014 (619 mm) and 2015 (639 mm) (Figure 28). The content of soil organic carbon was higher at the lower site (Site 2) than at the upper site (Site 1). Soil organic carbon content was positively correlated to clay content in the soils of the experimental sites (Table 7). The higher rice yield obtained at the lower site may be associated with higher organic carbon and clay contents. Variations in NERICA upland rice yields in northern Benin have been found to depend on pedoclimatic conditions mainly rainfall, soil organic carbon and clay contents (Worou, 2012).

At high nitrogen fertilizer level (120 kg N ha⁻¹), average grain yields of rice were 4.1 Mg ha⁻¹ at the upper site (Site 1) and 4.3 Mg ha⁻¹ at the lower site (Site 2). Average grain yields of rice under high nitrogen fertilizer level found in this study were within the range (4.0 – 5.6 Mg ha⁻¹) of maximum grain yield of upland rice obtained in experimental fields (Dingkuhn, Jones, Johnson, & Sow, 1998; Ekeleme et al., 2009; Kamara et al., 2010; Saito et al., 2006). At

zero-nitrogen fertilizer level, average grain yields of rice were low at the upper site (1.1 Mg ha^{-1}) and at the lower site (1.5 Mg ha^{-1}) and were within the range ($0.8 - 1.6 \text{ Mg ha}^{-1}$) of upland rice yields with zero or low amount of nitrogen fertilizer application (Saito et al., 2013). The large increases in rice yield following nitrogen application provide good evidence of the major role of this mineral nutrient in upland rice production in northern Benin. Similarly to the current results, Oikeh et al. (2008) reported 1.96 Mg ha^{-1} and 2.67 Mg ha^{-1} higher rice yield with 60 kg N ha^{-1} and 120 kg N ha^{-1} , respectively compared with the yields of zero-nitrogen fertilizer treatments in a Typic Haplustult in Nigeria.

The pattern of increase in grain yield caused by nitrogen fertilizer application and straw mulch points to the interactive mechanisms responsible for the crop responses to both factors on upland soils in northern Benin. Averaged over sites, tillage systems and nitrogen levels, application of 3 Mg ha^{-1} of rice straw mulch increased soil moisture by $0.010 \text{ m}^3 \text{ m}^{-3}$ and reduced soil temperature by $2.4 \text{ }^\circ\text{C}$ (Table 9). This might have alleviated the soil physical resistance to root development and increased root biomass and the response of rice plants to nitrogen fertilizer application as evidenced by higher agronomic use efficiency of nitrogen found under rice straw mulch and nitrogen fertilization (Table 22). Higher soil moisture and lower soil temperature are desirable soil conditions for upland rice production in the Savannah agro-ecological zone in West Africa where air temperatures are constantly high and water scarcity is a major constraint for crop production (Ereinstein, 2002). Similarly to the current results, Totin, Stroosnijder, and

Agbossou (2013) reported higher soil moisture content under rice straw mulch than non-mulch in upland rice fields in Benin. The differences in topsoil temperatures due to rice straw mulch found in this study are similar to those reported from Sahelian soils by Buerkert, Bationo, and Dossa (2000) with 2 Mg ha⁻¹ of millet straw and from Sub-humid soils of western Nigeria by De Vleeschauwer, Lal, and Malafa (1980) with 4 to 6 Mg ha⁻¹ of rice straw. Furthermore, the current results on the combined effects of rice straw mulch and nitrogen fertilizer application agree with the findings of Rahman, Chikushi, Saifizzaman, and Lauren (2005) who described higher soil moisture, grain yield and nitrogen use efficiency under rice straw mulch compared with bare soil in two consecutive years in an alluvial soil in Bangladesh.

Nitrogen application at 60 kg N ha⁻¹ combined with rice straw mulch achieved higher agronomic nitrogen use efficiency than 120 kg N ha⁻¹ combined with rice straw mulch (Table 22). This may be due to higher loss of nitrogen through nitrification and/or denitrification. Increases in N fertilization in most cases result in greater loss of N through N₂O emissions and nitrate leaching (Pelster et al., 2011).

The no-tillage and nitrogen fertilizer treatments exhibited significantly lower soil CO₂ emission per unit grain yield when compared with manual tillage and zero N fertilizer, but showed no significant difference in response to rice straw mulch (Figure 29). Thus, even though mulching treatments increased CO₂ emission to the atmosphere due to surface rice straw decomposition, the rice yield was higher due to ample supply of water and

better nitrogen use resulting in low amount of soil CO₂ emission per unit rice grain like previously reported by Liu et al. (2014).



**CHAPTER SIX: SUMMARY, CONCLUSIONS AND
RECOMMENDATIONS**

Summary

To explore effective ways to decrease soil CO₂ emission and increase soil carbon budget and grain yield, field experiments were conducted on two upland rice soils (Lixisol and Gleyic Luvisol) in northern Benin in West Africa. The specific objectives of the study were to examine the effects of tillage systems, rice straw mulch and inorganic nitrogen fertilizer application on soil CO₂ emission (i), on soil carbon budget (ii), to determine the factors controlling soil CO₂ emission (iii), and to identify appropriate combination of tillage systems, rice straw mulch and nitrogen fertilization to reduce soil CO₂ emission and increase soil carbon budget and upland rice yield in northern Benin (iv). The treatments comprised two tillage systems (no-tillage, and manual tillage), two rice straw managements (no rice straw, and rice straw mulch at 3 Mg ha⁻¹) and three nitrogen fertilizer levels (no nitrogen, moderate level of nitrogen: 60 kg ha⁻¹ recommended by the extension services in northern Benin, and high level of nitrogen: 120 kg ha⁻¹). Potassium and phosphorus fertilizers were applied to be non-limiting at 40 kg K₂O ha⁻¹ and 40 kg P₂O₅ ha⁻¹. Four replications of the twelve treatment combinations were arranged in a randomized complete block design. Soil CO₂ emission, soil moisture and soil temperature were measured at 5 cm depth in 6 to 10 days intervals during the rainy season and every two weeks during the dry season. At maturity, crop parameters measured included rice grain yield, above-ground biomass, and root-biomass. Soil carbon budgets were calculated to provide insights on whether the treatments resulted in net gains or losses of soil carbon.

The followings are the major results related to the first objective. No-tillage significantly reduced soil CO₂ emissions compared with manual tillage. Higher soil CO₂ emissions were recorded in the mulched treatments. Soil CO₂ emissions were higher in fertilized treatments compared with non-fertilized treatments.

The followings are the major results related to the second objective. Under the current practices of manual tillage, with no residue and no nitrogen fertilization in upland rice fields in northern Benin, the carbon added as aboveground biomass and root biomass was not enough to compensate for the loss of carbon from organic matter decomposition, rendering the upland rice fields as sources of atmospheric CO₂. With no-tillage, 3 Mg ha⁻¹ of rice straw mulch and 60 kg N ha⁻¹, the soil carbon budget was zero on the Lixisol and 0.6 Mg C ha⁻¹ on the Gleyic Luvisol. Under no-tillage, 3 Mg ha⁻¹ of rice straw mulch and 120 kg N ha⁻¹, the soil carbon budgets were positive on the Lixisol and on the Gleyic Luvisol.

The followings are the major results related to the third objective. Soil moisture was the main factor explaining the seasonal variability of soil CO₂ emission. Much larger soil CO₂ emissions were found in rainy than in dry season. During the rainy season, when the plant is grown, larger soil CO₂ emissions values were due to greater contribution from root respiration.

The followings are the major results related to the fourth objective. Rice yield was not significantly different as a function of tillage systems. On the contrary, rice yield significantly increased with application of rice straw mulch and nitrogen fertilizer. The highest response of rice yield to nitrogen

fertilizer addition was obtained for 60 kg N ha⁻¹ in combination with 3 Mg ha⁻¹ of rice straw mulch for the two tillage systems. Soil CO₂ emission per unit grain yield was lower under no-tillage, rice straw mulch and nitrogen fertilizer treatments. No-tillage combined with rice straw mulch and 60 kg N ha⁻¹ reduced soil CO₂ emission and increased soil carbon budget and upland rice yield in northern Benin.

Conclusions

Continuous rice cultivation under manual tillage and removal / burning of crop residues is detrimental to the soil and also negative for the environment and the crop yield. Adoption of appropriate tillage methods, crop residue application and proper fertilization are beneficial for the soil, the environment and the crop yield. These practices are also beneficial for resource-poor farmers by reducing the amount of inorganic fertilizer per unit of harvested product. This study showed that no-tillage, combined with rice straw mulch at 3 Mg ha⁻¹ and 60 kg N ha⁻¹ reduced soil CO₂ emission and increased soil carbon budget and upland rice yield in northern Benin.

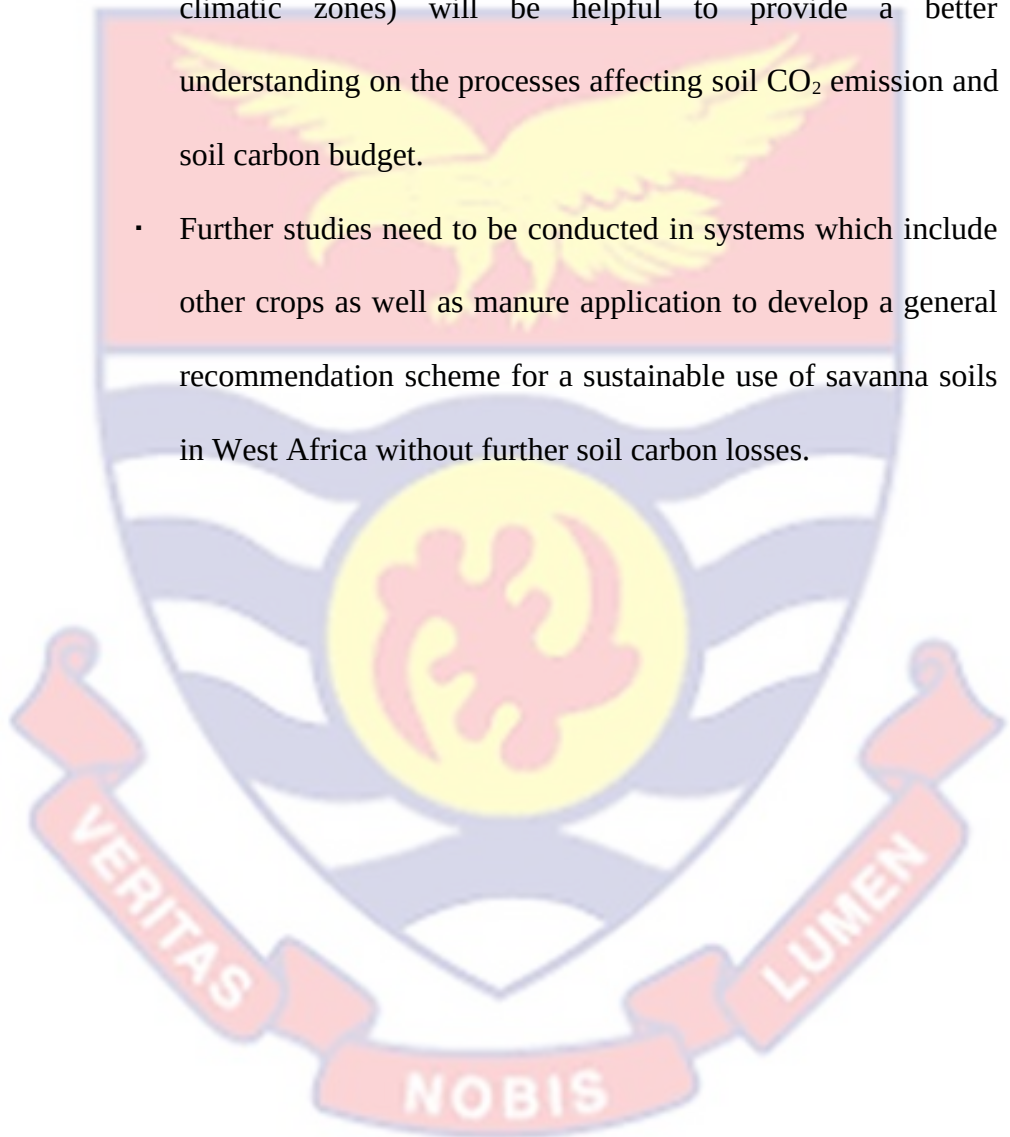
Recommendations

From the limitations of the study, the following recommendations are provided for further research.

- The findings of this study are for the first three years since the establishment of the treatments. Long-term studies will be

helpful to confirm the effects of the treatments on soil CO₂ emission, soil carbon budget and crop yields.

- A comparative study with different types of soil (Plinthosols, Cambisols) and at different climatic conditions (humid and arid climatic zones) will be helpful to provide a better understanding on the processes affecting soil CO₂ emission and soil carbon budget.
- Further studies need to be conducted in systems which include other crops as well as manure application to develop a general recommendation scheme for a sustainable use of savanna soils in West Africa without further soil carbon losses.



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APPENDICES

Appendix 1: Publications from this study

Peer reviewed journals

Dossou-Yovo, E.R., Brüggemann, N., Jesse, N., Huat, J., Ago, E. & Agbossou, E. (2016). Reducing soil CO₂ emission and improving upland rice yield with no-tillage, straw mulch and nitrogen fertilization in northern Benin. *Soil and Tillage Research*, 156, 44-53.

Dossou-Yovo, E.R., Brüggemann, N., Ampofo, E., Igue, M., Jesse, N., Huat, J. & Agbossou, E. (2016). Combining no-tillage, rice straw mulch and nitrogen fertilizer application to increase the soil carbon budget of upland rice yield. *Soil and Tillage Research*, 163, 152-159.

Dossou-Yovo, E.R., Ampofo, E., Igue, M., Sintondji, L., Naab, J., Huat, J. & Agbossou, E. (2016). Improving soil quality and upland rice yield in northern Benin with no-tillage, rice straw mulch and nitrogen fertilization. *International Journal of Agronomy and Agricultural Research*, 9, 117-131.

Poster

Dossou-Yovo, E.R., Brüggemann, N., Jesse, N., Huat, J., Ampofo, E., Ago, E. & Agbossou, E. (2015). Reducing soil CO₂ emission and improving upland rice yield with no-tillage, straw mulch and nitrogen fertilization in northern Benin. American Geosciences Union (AGU) General Assembly, San Francisco, California, USA, 14-18 December 2015.
<https://agu.confex.com/agu/fm15/meetingapp.cgi/Paper/63774>.

Oral communication

Dossou-Yovo, E.R., Jesse, N., Huat, J., Ampofo, E., Brüggemann, N. & Agbossou, E. (2014). Improving rice yield in Semi-arid zone of West Africa by combining no-tillage and fertilizers practices. *DIVECOSYS-CIRAD*, AfricaRice Center, Cotonou, Benin, 15-19 December, 2014.

