KWAME NKRUMAH UNIVERSITY OF SCIENCE AND TECHNOLOGY, KUMASI
COLLEGE OF AGRICULTURE AND NATURAL RESOURCES

FACULTY OF RENEWABLE NATURAL RESOURCES DEPARTMENT OF SILVICULTURE AND FOREST MANAGEMENT

SOIL RESPIRATION STUDIES IN TWO SITES OF DIFFERENT POST-LOGGING AGES IN A MOIST-SEMI DECIDUOUS FOREST IN GHANA

BY

ADU OPOKU-AMEYAW BSc. NATURAL RESOURCE MANAGEMENT KWAME NKRUMAH UNIVERSITY OF SCIENCE AND TECHNOLOGY, KUMASI

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF PHILOSOPHY IN SILVICULTURE AND FOREST MANAGEMENT

BY

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NOVEMBER, 2015

DECLARATION

I hereby declare that this submission is my own work towards the Mphil degree and that, to the best of my knowledge, it contains no material previously published by another person nor material which has been accepted for the award of any other degree of the University, except were due acknowledgement has been made in the text.

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ABSTRACT

A large proportion of carbon is stored up in forest soils. Nevertheless, carbon is also released into the atmosphere via soil respiration, a process which determines ecosystem function and a great contributor in the global carbon cycle. This study investigated soil respiration in the Bobiri Forest Reserve, a moist- semi deciduous forest in Ghana. The aim was to investigate the seasonality, magnitude and abiotic controls on total soil respiration and its component contributions from root-and-rhizosphere, mycorrhizae, surface litter and soil organic matter in a 12- and 55-year-old post-logged site over a full seasonal cycle. Soil respiration was measured at monthly intervals from May 2013 to April 2014, by means of a dynamic closed chamber method. Total soil respiration had a strong seasonal influence whereby average fluxes were higher during the wet season and lower during the dry season. Estimated total soil respiration was 18.03 and 17.83 Mg C ha^{-1} $year^{-1}$ at the 12- and 55-year-old sites respectively. In addition, estimated component contributions at the 12- and 55-year-old post-logged sites were 24.02 and 34.58 % for root-and-rhizosphere, 16.97 and 14.26 % for mycorrhizae, 27.42 and 25.17 % for litter and 31.59 and 25.99 % for soil organic matter, respectively. This depicted a higher autotrophic percentage at 55-year-old post-logged site (48.84 %) in comparison to 12-year-old post-logged site (40.99 %) and conversely, a higher heterotrophic percentage at 12-year-old post-logged site (59.01 %) in comparison to 55-year-old post-logged site (51.16 %). Relationship between soil respiration and soil moisture was quadratic, however observed variation was only explained at 12-year-old post-logged site ($R^2 = 0.75$; $p < 0.01$). A quadratic—quadratic regression of soil respiration and both soil temperature and soil moisture accounted for 83 % of observed variation in soil respiration at 12-year-old post-logged site ($p < 0.01$) but still did not improve variation at the 55year-old post-logged site ($p = 0.84$). The study shows the influence of forest age on soil respiration and confirms the importance of separating total soil respiration into source components. Thus, the information should serve as a

baseline for respiration studies in Ghana as well as assist in the understanding of forests and their influence on carbon cycling and global warming.

ACKNOWLEDGEMENTS

The research in this thesis is an adjunct of a FORIG-OXFORD project, 'Does shifting carbon use efficiency determine the growth rates of intact and disturbed tropical forests? Gathering new evidence from Africa', funded by the Natural Environment Research Council (NERC) (U.K). Work was also supported by an International Tropical Timber Organization (ITTO) fellowship award. I am very grateful to my supervisors, Dr. Kyereh Boateng (Senior Lecturer at the Department of Silviculture and Forest Management, Kwame Nkrumah University of Science and Technology) and Dr. Stephen Adu-Bredu (Principal Research Scientist of the Forestry Research Institute of Ghana (FORIG)) for their constructive comments, criticisms and corrections.

It would be very thoughtless if I do not also thank the many people who have in one way or another, helped me to complete this thesis. Sincere thanks and appreciation goes to Messrs Akwasi Duah-Gyamfi, Daniel Shalom Addo-Danso, Emmanuel Amponsah-Manu, Samuel Larbi, Mrs Gloria Djabletey and Dr. Kennedy Owusu-Afriyie all of CSIR-FORIG for their tremendous encouragement, immense support and invaluable suggestions. Also to Messrs. Micheal Adu Sasu, Adu-Gyamfi Asamoah, Kwabena Afriyie Agyekum, Mses. Forzia Ibrahim, Lydia Serwaa Bonsu and Rita Oppong Gyamfua, my close allies at the CUE lab (FORIG) who showed strong team spirit and support in field, lab activities as well as in data entry and analysis, I say a big thank you.

I also thank members of staff at the Department of Silviculture and Forest Management, most especially Dr. E.A. Abbeney for his encouragement and guidance.

My family has been my bedrock throughout my life and studies; most importantly my father, Dr. K. Opoku-Ameyaw, I am forever grateful for your prayers and unflinching support. Also to Dr. and Dr. Mrs. Derkyi (my auntie) and family I say a big thank you for all the kind support and encouragement.

Lastly, without my Heavenly Father, my life would be incomplete. I thank Jehovah God for the gift of life, undeserved kindness and for the protection He's bestowed upon me that has enabled me to complete this studies successfully

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CHAPTER ONE

1.0 INTRODUCTION

1.1 Background to the study

Recent decades have witnessed exertion by the scientific mainstream to better understand the role forest ecosystems play in mitigating global climate change and warming. On continental scales, profound research within various areas of study have surged, propelling the emergence and advancement in the use of cutting-edge methodologies such as micrometrological towers (e.g. Baldocchi *et al,* 2001), isotopic techniques (e.g. Buchmann *et al.*, 1997), CO_2 chamber based methods (e.g. Davidson *et al.*, 2002b), satellite based remote sensing (e.g. Verheggen, *et al.*,2012), climate-vegetation modeling (e.g. Potter *et al.*, 1993), in addition to *in situ* forest above- and belowground (e.g. Chave, 2005; Metcalfe *et al.*, 2007) mensuration techniques, for quantifying and monitoring forest carbon stocks and fluxes. This speedy transformation has come as no surprise because annual concentrations of atmospheric greenhouse gases (GHGs) continue to increase inexorably, at unprecedented rates with fears of doubling within the next century (IPCC, 2001).

Among the various GHGs, carbon dioxide (CO_2) is the most important individual gas (Smith *et al.,* 2003) responsible for trapping long-wave radiation and heating the earth's surface. The rise in its atmospheric concentration is one of the most documented phenomenon and daily continuous monitoring of its global levels, pioneered at Mauna Loa observatory in USA has shown a remarkable yearly rise from a 1958 level of 316 ppm (parts per million) to the current level of 399 ppm (as of July 2014) (source: http://www.esrl.noaa.gov/gmd/ccgg/trends/). Indeed, the current level and rate of increase within just 56 years are alarming, considering that CO_2 reconstruction studies indicate a lesser

concentration of *ca*. 280 ppm, thousands of years before the industrial revolution began (Barnola *et al*., 1987).

The glaring climatic consequences of atmospheric CO_2 levels are the warming of the earth's surface, melting of polar icecaps, and a rising sea level (Baldocchi *et al.,* 2001). In addition, elevated CO_2 studies particularly, free-air CO_2 enrichment (FACE) experiments point to a defect in plants' physiological and ecological functioning that include but not limited to reduced stomatal conductance and transpiration with ultimate increase in water-use efficiency, photosynthesis and light-use efficiency (Ainsworth and Long, 2005). For a certainty, the current rise in atmospheric CO_2 is due to human activities (IPCC, 2001), with the principal anthropogenic source being the combustion of fossil fuels for power generation, transport and industrial purposes (IPCC, 2001) with tropical deforestation and forest degradation in second place producing estimated emissions of 0.37 $PgCyr^{-1}$ (*ca*. 20 per cent) of global land use emissions (Ciais *et al*., 2011).

One major biospheric reservoir for carbon (C), which contains globally twice as much C as the atmosphere and three times as much as vegetation is soil (Han *et al.,* 2007). At the forest stand level, soils store a substantial amount of carbon which is an order of magnitude larger than or closer to the aboveground storage of carbon (Chiti *et al.,* 2010). Nevertheless soils release carbon dioxide back into the atmosphere through soil respiration. Globally, soil respiration is a great contributor in the terrestrial carbon cycle, being the second largest terrestrial carbon flux with annual releases following annual photosynthesis or gross primary production (GPP) (Litton *et al.,* 2011). At the forest stand level, soil CO_2 efflux accounts for 30-80% of total ecosystem respiration (Fenn *et al.,* 2010; Davidson *et al.,* 2006c). Therefore with this magnitude, small changes in soil respiration across large areas is expected to produce a great effect on atmospheric CO_2 concentrations by providing positive feedback effects and enhanced

soil respiration that may ultimately accelerate global warming (Raich and Schlesinger, 1992; Han *et al.*, 2007).

It is well recognized that tropical forests, despite covering merely 7–10% of the global land area (Lewis *et al.,* 2009), play a major role in the global carbon (C) cycle (Malhi and Grace, 2000). They store *ca*. 40% of the carbon residing in terrestrial vegetation and soil (Lewis *et al.,* 2009), while annually regulating this stock into the atmosphere as CO_2. The African tropical forests covering about 16% of the global forest area and being among the most pristine in the world are highly productive and contain large carbon stocks in their biomass of up to 255 Mg C ha^{-1} (Bombelli *et al.,* 2009; Ciais *et al.,* 2011). Paradoxically, this large store, especially in intact forests, is estimated to be increasing at a rate of 0.34 Pg C yr^{-1} (1 Pg=10^{15}gC) (Lewis *et al.,* 2009) despite ongoing deforestation. Thus, this reinforces confidence in the carbon sink strength of African tropical forests. Nevertheless, like all tropical forests, there remains some form of uncertainties as to the consistency of this sink strength, particularly in response to changes in climate (Cowling *et al.,* 2004). In contrast to tropical Amazonia and the other forest biomes such as temperate forests, comprehensive studies on belowground carbon cycling in tropical African forests, (particularly forests of Central and West Africa (Guineo-Congolian region)) is limited in scope (Mahli *et al.,* 2013).

Soil respiration, variably referred to as soil carbon dioxide efflux or belowground respiration, is a complex process originating from respiration of plant root and its associated mychorrhizae and the microbial breakdown of organic matter (Subke *et al.,* 2006). Soil respiration and its source components are controlled and may respond differently to a suite of biotic and abiotic factors and their interactions. Although soil temperature (Lloyd and Taylor, 1994; Fang and Moncrieff, 2001) and moisture content (Davidson *et al.,* 2000; Schwendenmann *et al.,* 2003)

are recognized as the most important controlling factors, several other factors such as relative supply of photosynthate from aboveground vegetation

(Högberg *et al.,* 2001; Johnsen *et al.,* 2007), vegetation type (Raich and Schlesinger, 1992; Han *et al.,* 2014) land use management and/or disturbance regimes (Epron *et al.,* 2006; Sheng *et al.,* 2009) and stand age (Jassal *et al.,* 2012; Wang et *al.,* 2013) have been found to have a controlling effect. Variation of these factors will characterize, for a specific ecosystem, the magnitude, temporal and spatial variability in soil respiration (Han *et al.,* 2007) which would in turn determine whether an ecosystem is a net source or sink of CO_2 (Metcalfe *et al.,* 2007). Soil respiration and its partitioning into its component fluxes is important for assessing plant physiology, C allocation, ecosystem C balance, and the climate feedback potential of changes in soil respiration (Bond-Lamberty *et al.,* 2010).

1.2 Problem statement

Ghana's tropical forest area covers *ca*. 4,939,958 hectares or *ca*. 21.7% of the total land area (FAO, 2010), hence would have significant implications in the global carbon cycle, as well as climate change mitigation. However, there have been few mechanistic studies on carbon dynamics which have been centered mostly on aboveground stocks and the vulnerability of these carbon stocks to disturbance such as selective logging, forest conversion and climate change (e.g. Gineste *et al.,* 2008; Adu-Bredu *et al.,* 2008). Studies on belowground carbon dynamics is scarce, with the few rather restricted to agricultural, agroforestry and forest plantations ecosystems (e.g. Isaac *et al.,* 2005; Asase *et al.,* 2008; Ofori-Frimpong *et al.,* 2010). Again, the few studies that have been accomplished in selected natural forest ecosystems have focused on stocks (e.g. Dawoe, 2009; Chiti *et al.,* 2010) with inadequate information of the fluxes of carbon. The existing status quo, inter alia, could be attributed to the dearth of logistics and high cost associated with research in forest ecosystems.

1.3 Justification of study

Accurate quantification of C fluxes, particularly soil respiration remains an important step towards advancing our understanding of the carbon cycle of Ghana's forests. Furthermore,

Ghana as a country is a signatory to the United Nations Framework Convention on Climate Change (UNFCCC) and has taken a proactive step towards initiating the Reduced Emissions from Deforestation and Forest Degradation Plus (REDD+) preparedness programme, which is a strategy to better manage its forest resources and mitigate climate change. In the context of the REDD+ initiative, it is important to quantify both the carbon stocks and the carbon fluxes of African forests (Ciais *et al.*, 2011). Therefore, in light of this pressing research need, a study of this nature will be crucial to help in a better understanding the fluxes and allocation of carbon in Ghana's forest. This will unearth the underlying responses of belowground components to the carbon cycle. Data obtained will also provide baseline estimates of current forest belowground cycling, as well as serve as a focus for a more comprehensive assessment of the entire carbon budget of Ghana's tropical forests. Knowledge of atmospheric-biosphere modeling will be further deepened and results obtained will contribute towards local, regional and international decisions on climate monitoring as well as policy formulation and implementation.

1.4 Objective of research

The overarching objective of this research was to investigate the dynamics of belowground carbon dynamics via the study of trends and patterns in soil respiration over one full seasonal cycle in a 12- and 55-year-old post-logged sites in the Bobiri Forest Reserve, a moist- semi deciduous forest in Ghana. The specific objectives were to:

1. Assess the seasonality of soil respiration and its component (ground-litter, root and their rhizosphere, mycorrhizae, and soil organic matter) respiration at each site.

2. Quantify the magnitude of annual total soil respiration and component contributions at each site.
3. Determine the response of total soil respiration to changes in soil temperature and soil moisture.

1.5 Research questions

The questions that guided the study were:

- Does total soil respiration as well as each component respiration remain invariant over the year or do they vary seasonally at each site?
- What is the annual magnitude of total soil respiration and percentage contributions from ground-litter, root and their rhizosphere, mycorrhizae, and soil organic matter decomposition at each site?
- Which of the abiotic factors strongly influences total soil respiration at each site?

1.6 Hypotheses

H1: There exists a strong seasonal variation in total soil respiration and component respiration at each site.

H2: There is no significant difference in the annual magnitude of total soil respiration and component respiration between the two sites.

H3: There exists a strong relationship between soil respiration and either soil temperature or soil moisture at each site.

CHAPTER TWO

2.0 LITERATURE REVIEW

2.1 Soil respiration and component fluxes

Soil respiration is the production and release of CO_2 as a by-product of metabolism of soil living organisms (autotrophs and heterotrophs) yielding energy and/or carbon intermediates for maintenance, growth, ion uptake and reproduction of organisms (Luo and Zhou, 2006). Autotrophic organisms include plant roots (the major contributor) and algae and chemolithotrophs both of which are of minor significance (Kuzyakov, 2006). Important heterotrophs include soil microorganisms made up of bacteria, fungi, actinomycetes and protozoans that are responsible for most CO_2 efflux by heterotrophs (Luo and Zhou, 2006). Although contribution by soil macrofauna (i.e. macroscopic invertebrates and small mammals) to heterotrophic respiration is minimal, they play a major role through fragmentation and comminution of soil organic matter into minute particles for improved microbial attack and or preying on some groups of micro-organisms (Killham, 1994; Bonkowski, 2004; Kuzyakov, 2006),

In partitioning soil respiration, Subke *et al.* (2006) and Kuzyakov and Gavrichkova (2010), considered total soil respiration to be a result of several sources namely: (1) microbial decomposition of soil organic matter (SOM) (basal respiration), (2) microbial decomposition of SOM affected by recent input of rhizodeposits or/and fresh plant residues (priming effect), (3) microbial decomposition of dead plant (shoot and root) remains, (4) microbial decomposition of rhizodeposits of living roots, also 'rhizomicrobial respiration' and (5) root respiration.

Nevertheless, the exact categorization of source components into autotrophic and heterotrophic components of soil respiration remains a challenge and is still under debate (Heinemeyer *et al.*, 2012). For instance, Kuzyakov and Gavrichkova (2010) categorized respiration by

heterotrophs as all sources of microbial activities, and root respiration as respiration by autotrophs. This is because *sensu stricto,* roots are the only soil autotrophs, with heterotrophic microorganisms responsible for all microbial decomposition in addition to rhizomicrobial respiration which is caused by decomposing rhizodeposits in the rhizosphere.

However, other researchers (Sulzman *et al.,* 2005; Högberg *et al.,* 2004; Gaumont-Guay *et al.,* 2007; Subke *et al.,* 2006; Heinemeyer *et al.,* 2012) have preferred autotrophic component as actual root respiration in addition to rhizomicrobial respiration due to fact that many soil organisms especially mycorrhizal fungi are multifunctional, in that, they form symbiotic associations with root systems and access carbon sources from both GPP and litter decomposition (Staddon *et al.,* 2002; Lindahl *et al.,* 2007; Heinemeyer *et al.,* 2012), hence leading to a not so abrupt boundary between root and rhizomicrobial respiration (Kuzyakov, 2006). Therefore, Högberg *et al.* (2004) differentiated organisms that receive photosynthates more or less directly from the plant canopy as functional autotrophs and organisms that receive their carbon mainly through decomposition of dead or dying organic matter as functional heterotrophs. On the other hand, many studies have employed the generic term ‘rhizospheric or ‘root-rhizosphere’ respiration to describe all sources of CO_2 production in the rhizosphere (i.e. root itself and its zone of influence, including closely associated microorganisms living on rhizodeposits and the sheath of mycorrhizal fungi around the root) (Wang and Yang, 2007; Fenn *et al.,* 2010; Malhi *et al.,* 2014; da Costa *et al.,* 2014; Doughty *et al.,* 2014; Huasco *et al.,* 2014). Heterotrophic respiration is then restricted to soil respiration that originates from the metabolic activity of “free-living” soil organisms that decompose SOM and litter inputs. Still, Moyano *et al.* (2008) in their partitioning of soil respiration fluxes further distinguished between rhizosphere respiration and autotrophic respiration (referred to as

mycorrhizosphere respiration), where the later was defined as the rhizosphere plus the extra radical mycelia of mycorrhizal fungi.

The contribution of the various source components to total soil respiration has been studied and many studies generally suggest considerable contributions from different components. For example, Hanson *et al*. (2000) reviewed partitioning methods and reported that the annual contribution of root respiration to total soil respiration from different studies ranges from as low as 10 to as high as 90% in forest stands. Across four sites of a tropical forest ecosystem, Metcalfe *et al.* (2007) found mean contributions of respiration from litter, roots, and SOM to range between 5–13%, 40–75% and 14–54% of total soil respiration, respectively. Fenn *et al.* (2010) partitioned soil respiration into SOM decomposition, rootand-rhizosphere, and mycorrhizal respiration to be 70, 22 and 8 % total soil respiration, respectively for a temperate deciduous forest. Heinemeyer *et al.* (2012) reported annual fluxes of roots, mycorrhizal and heterotrophic fluxes to contribute 38, 18 and 44 %, respectively in a temperate deciduous oak forest in South East England.

2.2 Spatial and temporal characteristics of soil respiration

The temporal and spatial variation of soil respiration has been well documented revealing that soil respiration greatly varies with time (temporal) and space (spatial) (Luo and Zhou, 2006). The temporal and spatial variation in soil respiration is to a large extent driven by the effect of variation in soil temperature and moisture. In most ecosystems, temporal variation in soil respiration can be characterized diurnally/weekly, seasonally, interannually, and decadal/centennially (Luo and Zhou, 2006). On the other hand, soil respiration is related to physical and chemical conditions of the soil hence spatial heterogeneity of soil respiration and its temporal variation could as well be explained by variation in root biomass, microbial

biomass, surface litter amount, soil organic carbon (SOC), soil total nitrogen (Total N), cation exchange capacity, soil bulk density, soil porosity, soil pH and site topography (Hanson *et al.*, 1993; Qi and Xu, 2001; Epron *et al.*, 2004; Luo *et al.*, 2012).

Seasonal variation in soil respiration in many ecosystems is driven by seasonal change in precipitation patterns, soil moisture, soil temperature, photosynthate production and/or their combinations (Luo and Zhou, 2006). In temperate and boreal forest ecosystems, a seasonal change in temperature is normally a stronger controlling factor than moisture content (e.g., Fenn *et al.*, 2010; Heinemeyer *et al.*, 2012). Conversely, a change in moisture content and precipitation is the main controlling factor influencing seasonal variation in soil respiration in tropical forests. In tropical forests, where precipitation is highly seasonal and/or a clear phase-locked dry period could be detected, soil respiration is normally observed to exhibit a clear seasonal pattern whereby soil respiration increases during the wet seasons when precipitation is high and decreases during the dry season when precipitation is low (e.g. Davison *et al.*, 2000; Valentini *et al.*, 2008). In contrast, in tropical aseasonal forests where both seasonality in temperature and precipitation/moisture are favorable all year round, it is difficult to distinguish a clear temporal pattern in soil respiration (e.g. Schwendennman *et al.*, 2003; Ohashi *et al.*, 2008; del Aguila-Pasquel *et al.*, 2014).

In addition to total soil respiration, many studies have reported seasonality in component fluxes of soil respiration (e.g. Sulzman *et al.*, 2005; Högberg *et al.*, 2005; Gaumont-Guay *et al.*, 2007; Metcalfe *et al.*, 2007; Fenn *et al.*, 2010; Heinemeyer *et al.*, 2012). For example, plant root respiration is dependent on the supply of carbohydrate from photosynthesis to roots (Poorter *et al.*, 1991). Therefore in tropical forests, greater fluxes of respiration from roots and their rhizosphere occurs in the growing season and is usually low during the dormant season, when carbohydrate supply from canopy photosynthesis and tree physiological activities is low (Luo and Zhou, 2006).

Spatial variation in soil respiration occurs on various scales, from a few square centimeters to several hectares (ha) up to the globe (Luo and Zhou, 2006). At the forest stand level, spatial variation could be large even in relatively homogeneous site (Davidson *et al.,* 2002b). The high spatial variability in soil respiration results from large variations in soil physical properties (e.g. soil water content, thermal conditions, texture, porosity and chemistry), biological conditions (e.g. fine-root biomass, tunneling soil animals, bacteria and fungi), nutrient availability (e.g. deposit litter and nitrogen mineralization) and others (e.g. disturbed history and weathering) (Luo and Zhou, 2006). For example, Ohashi *et al.* (2008) observed relatively high spatial variability in soil respiration in an aseasonal tropical forest in Malaysia. Spatial variability was reduced after removal of relatively high fluxes, which was attributed to hotspots resulting from mobile factors such as nesting and foraging activity of termites and/or ants. In addition, the authors found that spatial variation in soil CO_2 efflux could also be explained by local spatial differences in temperature. It was suggested that the unevenness of canopy structure and underground vegetation generates heterogeneity in the sun's radiation reaching the forest floor, leading to patchiness in temperature in the litter and soil surface layers. Also, Metcalfe *et al.* (2007) observed considerable within-site spatial heterogeneity in soil respiration in four rain forest sites in the eastern Amazon whereby the observed variation could not be explained by temperature or moisture. Within site spatial variation was only explained by root and litter mass and their specific respiration rates.

2.3 Factors influencing soil respiration

Soil respiration is controlled by a suite of factors which include soil temperature (Lloyd and Taylor, 1994; Fang and Moncrieff, 2001) and soil moisture content (Davidson *et al.,* 2000; Xu and Qi, 2001) as well as other factors like soil nutrient availability (Raich and

Tufekcioglu, 2000), relative supply of photosynthate from aboveground (Högberg *et al.,* 2001; Johnsen *et al.,* 2007), root biomass (Ohashi *et al.,* 2000; Metcalfe *et al.,* 2007) and land use and disturbance regimes (Epron *et al.,* 2006; Sheng *et al.,* 2009).

2.3.1 Soil temperature dependence on soil respiration

Temperature is recognized as a major environmental factor influencing soil respiration. Low temperatures can limit the capacity of both soluble and membrane-bound enzymes. However, at extremely higher temperatures, enzymes associated with the biological process may be deactivated or 'killed'. The relationship between soil respiration and temperature has widely been described by a simple exponential equation proposed by Van't Hoff (1884) or an Arrhenius modification (Llyod and Taylor, 1994; Table 1). However different types of empirical models have also been used in modeling the dependence of temperature on soil respiration and these include the Llyod and Taylor model (Llyod and Taylor, 1994), linear models (Chambers *et al.,* 2004), quadratic models (Holthausen and Caldwell, 1980) and logistic models (Jenkinson, 1990; Yu *et al.,* 2011).

2.3.2 Soil moisture dependence on soil respiration

Soil moisture is another important abiotic factor which influences soil respiration. Soil respiration can be extremely altered by soil moisture since moisture affects rooting depth, root respiration and soil microbial community composition. Soil respiration is low in dry conditions, increasing at intermediate moisture levels, reaching a plateau at optimum moisture levels and decreasing at high soil moisture contents (Linn and Doran, 1984; Tang and Baldocchi, 2005). At supra-optimum soil moisture levels, soil respiration will decrease with increasing soil moisture, mainly due to reduced oxygen availability, which limits microbial decay of SOM (Moyano *et al.,* 2013). When soil moisture decreases below optimal levels, soil

respiration reduces due to low root respiration (Burton *et al.,* 1998; Heinemeyer *et al.,* 2012) resulting from reduced root growth and ion uptake, as well as reduced maintenance costs following protein degradation, lower membrane potentials and increased root death (Burton *et al.,* 1998). However in ecosystems with high root densities, the effect of moisture limitation can be decoupled due to deeper roots water uptake from deeper soil layers, thereby maintaining root-rhizosphere functioning (hydraulic redistribution) (Nepstad *et al.,* 1994; Chen *et al.,* 2010c). In addition, dry soils can limit heterotrophic respiration by limiting microbial mobility and the diffusion of extracellular enzymes produced by microbes for the breakdown of organic matter and the diffusion of soluble C substrates that can be assimilated by microbial cells within the liquid phase of the soil (Linn and Doran, 1984; Davidson *et al.,* 2006a). Hence, rewetting dry soils particularly by rainfall events after drought increases soil respiration considerably (that is the "Birch effect"), due to the increase of microbial activity arising from dead microbial cells accumulated during the drought, and/or the release of organic solutes from live and dead cells following wetting that increases soil heterotrophic respiration (Birch, 1958; Borken, 2003; Savage and Davidson, 2003; Jarvis *et al.,* 2007).

The response of soil respiration to changes in soil moisture has been described by several equations, including linear (Davidson *et al.,* 1998), curvilinear (Chambers *et al.,* 2004), parabolic (Schwendenmann *et al.,* 2003; Sotta *et al.,* 2004; Valentini *et al.,* 2008) and exponential (Davidson *et al.,* 2000) with functions of soil water expressed as matric potential, gravimetric water content and volumetric water content (Table 1).

2.3.3 Confounding dependence of soil temperature and soil moisture on soil respiration

Soil respiration is often interactively affected by both soil temperature and soil moisture and in some cases it is difficult to separate their interactions (Davidson *et al*., 1998: Lou and Zhou, 2006). Soil respiration, like many other physiological processes of plants and microbes, would

usually respond to the most limiting factor (Lou and Zhou, 2006). Soil respiration is not sensitive to moisture under low temperatures but more responsive at high temperatures (Lou and Zhou, 2006). Again soil respiration is more responsive to soil temperature under optimum moisture (Harper *et al.*, 2005). However, when both temperature and moisture are not at their extremes, both can interactively influence soil respiration and account for most of its observed variability (Lou and Zhou, 2006). For example Davidson *et al.* (1998) observed the effects of temperature and water content to confound in the soils of a temperate forest in New England, where the summers are warm with dry periods and the winters are cool and wet.

The response of soil respiration to both soil temperature and soil moisture has been described by several equations in numerous studies (Table 1). In most cases, it involves a multiplicative model of both soil temperature and moisture models.

Table 1: Examples of some empirical equations used to describe the relationship of soil respiration with soil temperature and soil moisture.

Function name	Equation	Reference
Respiration-temperature		
Arrhenius	$R = ae^{-Ea/RT}$	Arrhenius (1898)
van't Hoff (First-order exponential)	$R = ae^{bT}$	van't Hoff (1884)

Modified van't Hoff	$R = R_o \times Q_{10((T-T^o)/10)}$	van't Hoff (1898)
Lloyd and Tailor	$R = ae^{-Ea/(T-To)}$	Lloyd and Tailor (1994)
Second-order exponential	$R = ae^{bT+cT^2}$	O'Connell (1990)
Linear	$R = a + bT + c$	Rochette *et al.* (1997)
Quadratic	$R = aT^2 + bT + c$	Lovelock (2008)
Varying power	$R = a(T + 10)^b$	Kucera and Kirkham (1971)
Logistic	$R = 1/(a + b^{-((T-10)/10)})$	Jenkinson (1990)
	$R = a/\ (1 + \exp(b(c - T)))$	Yu *et al.* (2011)
Respiration-moisture		
Linear	$R = a + b\Psi + c$	Davidson *et al.* (2000)
Exponential	$R = ae^{b\Psi}$	Davidson *et al.* (1998)
Quadratic	$R = a\theta^2 + b\theta + c$	Schwendenmann *et al.* (2003) Sotta *et al.* (2004)
Hyperbolic	$R = a + b\theta + c/\theta$	Gaumont-Guay *et al.* (2006)
Modified Bunnell	$R = a(\theta/(b + \theta))(c/(c + \theta))$	Gaumont-Guay *et al.* (2006)
Respiration-temperature and moisture		
Exponential-exponential	$R = (ae^{bT})(ce^{d\Psi})$	Davidson *et al.* (1998)
	$R = (ae^{bT})(ce^{d\theta})$	Lai *et al.* (2012)
Exponential- quadratic	$R = (ae^{bT})(c\theta + d\theta^2)$	Campos (2014)
Lloyd and Tailor -quadratic	$R = (ae^{-Ea/(T-To)})(c\theta + d\theta 2)$	Zimmermann *et al.* (2009)
Bunnell	$R = (\theta/a + \theta)(b/b + \theta)cd^{((T-10)/10)}$	Bunnell *et al.* (1977) Valentini *et al.* (2008)

R is soil respiration, *T* is soil temperature, **θ** is volumetric or gravimetric soil moisture, **Ψ** is soil matric potential and *E* is activation energy. Parameters a, b, c and d are model parameters estimated by regression analysis.

2.4 Effects of logging on soil respiration

Many logging studies have focused on the effect of clear-cutting on soil respiration and these studies have reported the magnitude of soil respiration to immediately decrease (e.g. Popescu, 2001; Epron, 2006), increase (e.g. Ewel *et al.*, 1987; Lytle and Cronan, 1998) or show no

significant change (e.g. Toland and Zak, 1994) in sites following clear-cutting. However, the timing and strength of soil respiration seems rather site specific and depends greatly on the level of disturbance, the type and intensity of harvest and the extent to which biotic and abiotic parameters are affected by disturbance (Wiseman, 2001).

In Ghana, the main type of logging mostly done in forest reserves is selective logging which is variably referred to as the polycyclic logging system. This serves as the main means of timber extraction and silvicultural treatment (Hawthorne *et al.*, 2011). As the name implies trees which are of commercial value and of merchantable diameter are purposely selected for felling and involves the periodic entries into a given forest area for extraction (Duah- Gyamfi, 2007). Selective logging by means of its operations impact soil physical and chemical properties via the use of modern heavy harvesting machines which introduces compaction and top soil removal (Abebrese and Kyereh, 2005). Direct compaction impacts include increased bulk density which in turn leads to reduced soil macroporosity and water retention and infiltration capacities which limit aeration and root penetration (Hendrison, 1990; Abebrese and Kyereh, 2005). Increased bulk density as a result of compaction can influence soil respiration by reducing pore spaces which facilitates diffusion of gases (Linn and Doran, 1984; Davidson and Trumbore, 1995). Besides, limited aeration as a result of low oxygen availability and low water infiltration could lead to reduced microbial activities and reduced root penetration could result in root and mycorrhizae mortality (Chen *et al.*, 2010b; Luo *et al.*, 2012). All these will in turn lead to low heterotrophic and autotrophic respiration.

Secondly, the removal of trees leads to canopy openings which facilitate greater solar radiation reaching forest floor, hence affecting abiotic factors such as ground surface temperatures and decreased soil moisture (Swaine and Whitmore, 1988; Agyemang *et al.*, 1999). Extremes in soil temperatures and moisture availability would affect microbial composition and activities. In addition increased transpiration resulting from temperatures would affect root respiration

due to low root growth and ion uptake (Burton, 1998). In addition, tree removal which inputs a large amount of forest litter, course woody debris and dying tree roots would increase heterotrophic respiration as a result of enhanced microbial decomposition from priming effects (Sayer *et al.*, 2007).

2.5 Effects of forest age and succession on soil respiration

At longer time scales, soil respiration and its components changes with stand age, but results have varied. Martin *et al.* (2007) using a chronosequence of three sites of different ages (24, 81 and 277 years following natural burning) in a cool temperate mountain ash (*Eucalyptus regnans*) forest in south-eastern Australia, observed that soil respiration increased from 2.9 μmol CO_2 m^{-2} s^{-1} in the youngest site to 5.3 μmol CO_2 m^{-2} s^{-1} in the old-growth site. The highest rate in the old-growth site was as a result of greater root biomass, highest concentration of oxidisable organic carbon and nitrogen which in turn drives root turnover and SOM decomposition. In contrast, Saiz *et al.* (2006) found total soil respiration to decrease with age over a Sitka spruce chronosequence (10, 15, 31 and 47 year old) plantation established in Central Ireland. In their case, the relative contribution of both autotrophic and heterotrophic respiration decreased with stand age which was explained by a decrease in fine root biomass and activity with aging. Similarly Jassal *et al.* (2012) observed soil respiration in a 21-year-old Douglas-fir stand to be higher than in a 60-year-old stand in Canada.

Whereas gross primary photosynthesis was lower at the younger site, they attributed the higher respiration rate to abundant deciduous understory and a relatively thicker Litterfermenting-humified layer which influenced at the younger stand.

The contribution of autotrophic respiration was found to increase with stand age in *Pinus elliottii* plantations in Florida, from 51% in a 9-year-old stand to 62% in a 29-year-old stand.

This was explained primarily by the nearly threefold increase in live root biomass (Ewel *et al.*, 1987). Similarly, in black spruce chronosequence (4, 7, 13, 21, 38, 72 and 152 year-old), an increase in autotrophic respiration to soil respiration with stand age was reported however, a lower autotrophic respiration in the oldest stand (152-year-old) was attributed to a decrease in primary production (Bond-Lamberty *et al.*, 2004). Also according to Epron (2009), total soil respiration decreased with stand age for a Eucalyptus plantation in Congo. In the younger stand, heterotrophic respiration from decomposition of residues is higher than in other stands.

Similarly, in a vegetation succession study conducted in different stages of succession on Glacier forehead in China, Luo *et al.* (2012) observed soil respiration to increase with succession from a site dominated by pioneers to that occupied by climax species. The increase in soil respiration was attributed to specific microbial respiration (microbial respiration rate/unit microbial biomass) which in turn can be attributed to an increase in organic matter input via litterfall and root mortality among successional site.

2.6 Soil respiration measurement methods

Soil respiration measurement techniques could be broadly categorized into direct and indirect methods (Lou and Zhou, 2006). Indirect methods involve the use of other measured parameters to estimate soil CO_2 efflux. Direct methods quantify soil respiration by measuring changes in CO_2 concentration emitted from the soil surface using chambers methods or within the soil using CO_2-well (flux gradient) methods (Luo and Zhou, 2006; Figure 1). Chamber method, as the name implies, employs the use of soil chambers that are placed directly on an area of soil surface for the measurement of soil respiration. CO_2-well method on the other hand, eliminates the use of chambers and involves the use of solid-state CO_2 sensors to measure soil respiration based on Fick's fist law of diffusion, where the CO_2 fluxes within the soil profile are measured

at two or more depths (Davidson and Trumbore, 1995; Risk *et al.*, 2002; Vargas and Allen, 2008; Johnson *et al.*, 2013).

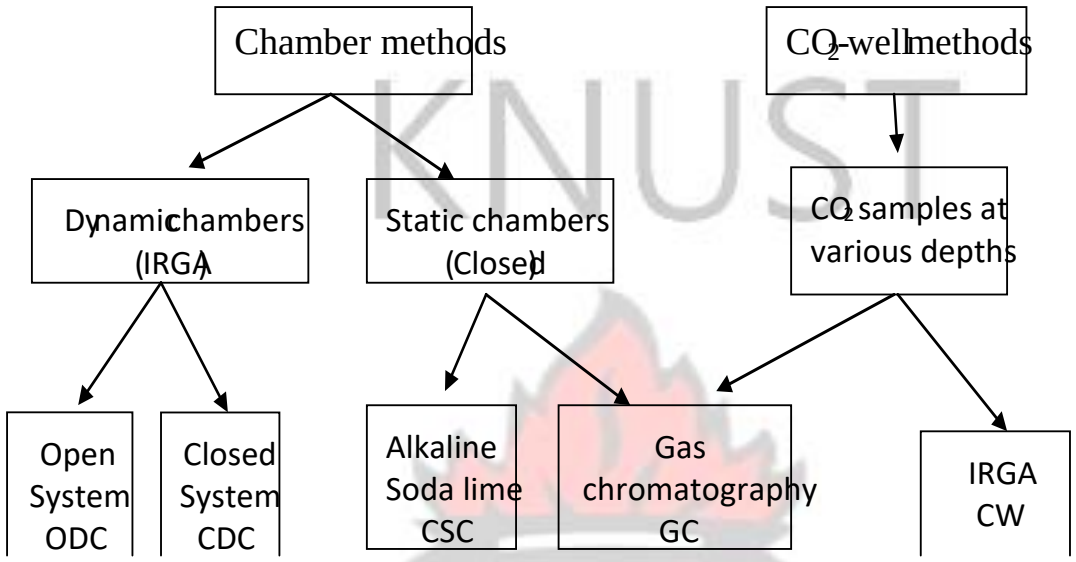


Figure 1: Classification of direct methods of measuring soil respiration. Adapted from Luo and Zhou, 2006.

Based on the presence or absence of air circulation, chamber methods are either dynamic or static (Janssens *et al*, 2000; Luo and Zhou, 2006). Dynamic systems circulate sampled air from a soil chamber to an infrared gas analyzer (IRGA), which measures CO_2 concentration by passing infrared light through a cylinder containing the sampled air. By computing the change in CO_2 concentration over a specific time period, a soil respiration rate is derived.

In the closed dynamic chamber (CDC) system, sampled air is allowed to circulate from the chamber to an external IRGA and then back to the chamber (Rochette *et al.*, 1997). The open dynamic chamber (ODC) system, on the other hand, vents sampled air to the atmosphere instead of being returned to the chamber (Rayment and Jarvis, 1997).

Finally, in the static chamber method, an area of soil surface is covered with a chamber while having a chemical absorbent inside the chamber to absorb CO_2 molecules. Within a specified

time period, soil respiration can be measured. Based on the chemical used, traditional static methods can be either alkaline (NaOH or KOH solutions) absorption or soda lime (a mixture of sodium and calcium hydroxides). Alternatively, gas could be sampled at time intervals using syringes and brought back to the laboratory for analysis with a gas chromatography (GC) or infrared gas analyzer (IRGA) (Luo and Zhuo 2006) .

2.7 Soil respiration partitioning methods

There has been a proliferation of soil partitioning research involving different methods with several reviews on the methods and challenges (Hanson *et al.,* 2000; Baggs, 2006; Kuzyakov, 2006; Subke *et al.,* 2006; Luo and Zhou, 2006). The methods that have been used have either been direct or indirect. Indirect methods have been mostly component mass linear or exponential regression which correlates soil respiration at a given location with the root biomass or soil organic matter at the same location (Rodeghiero and Cescatti, 2006; Bao *et al.,* 2010; Ferrea *et al*., 2012). The variation in soil respiration is then assumed to be due to the variation in root content or soil organic carbon. Hence, in the event that variations of soil respiration depend on the spatial variability of root density or soil organic carbon only, the yintercept of the extrapolated regression line gives the portion of autotrophic respiration or heterotrophic respiration respectively

Direct methods on the other hand, involve direct measurement of components and these include methods like component integration (Hanson *et al.,* 2000; Baggs, 2006) which involves the separation of soil components contributing to soil respiration (i.e., roots, litter, mycorrhizal hyphae and SOM), measurements of the specific rates of CO_2 efflux per unit mass for each component and subsequently summing up the various component fluxes to yield an integrated total of soil respiration (Hanson *et al.,* 2000; Luo and Zhou, 2006; Baggs, 2006). Root contribution to soil respiration has involved root excision and respiration taken before roots

transubstantiate (Burton *et al.*, 1998). However the technique is noted to cause severe root damage and drastically alter the rhizosphere environment such as mycorrhizae, O_2 and CO_2 concentrations (Hanson *et al.*, 2000; Luo and Zhou, 2006). Another approach has been the careful excavation of entire roots (including fine roots) which are enclosed in a cuvette while still attached to the plant and root respiration measured directly (Kutsch *et al.*, 2001).

Also root exclusion method has been employed using either trenching or root removal (Ewel *et al*., 1987; Gaumont-Guay *et al.*, 2007; Butler *et al.*, 2012). Trenching involves digging or in most recent studies inserting deep PVC below the rooting depth, around a core of soil to kill existing roots and mycorrhizal hyphae hence precluding root regrowth. However, the main disadvantage associated with trenching is the decomposition of residual decomposing severed dead roots which is corrected by removing roots from the excavated soil and placing soil back in reverse order of removal (Heinemeyer *et al.*, 2012). Also stem girdling that involves the removal of the bark of trees around the circumference of trees (Högberg *et al.*, 2001; Chen *et al.*, 2010a) or the use of cold-blocks by chilling the stems (phloem) (Johnsen *et al.*, 2007) has been used to exclude roots by disrupting the transport of assimilates from the crowns to the roots in the phloem.

To quantify ground surface litter contribution to soil respiration, manipulations have been done where litter is either removed via placing litter traps over the litter treatment plots, or by manual removal of existing litterfall. Litter contribution is estimated by subtracting CO_2 efflux rates measured in the plots with litter removal from the rates in the control plots in which litter is allowed to accumulate normally (Sayer *et al.*, 2007)

Finally, isotopic labelling of different soil components has also been used in partitioning total soil respiration. The methods included pulse- labelling with ^{14}C (Horwath *et al.*, 1994; Carbone *et al.*, 2007) or ^{13}C (Plain *et al.*, 2009; Högberg *et al.*, 2010), continuous labelling (Liljeroth *et*

al., 1994), atomic bomb-derived ^{14}C (Dorr and Munnich, 1987), stable isotope techniques (Trumbore *et al.*, 2006) and free air CO_2 enrichment (Ellsworth, 1999). The main advantage is that the methods introduce minimal disturbance to the soil system however, the methods are time consuming and expensive.

CHAPTER THREE

3.0 MATERIALS AND METHODS

3.1 Study area

3.1.1 Location

This study was conducted at the Bobiri Forest Reserve (BFR) (Figure 2). The reserve is located approximately 30 km east of Kumasi, Ghana and lies between latitude 6^0 39' and 6^0 44' North of the Equator and longitudes 1^0 15' and 1^0 23' West of the Greenwich. The Reserve is situated in the Ejisu-Juabeng District but it is under Juaso Forest District.

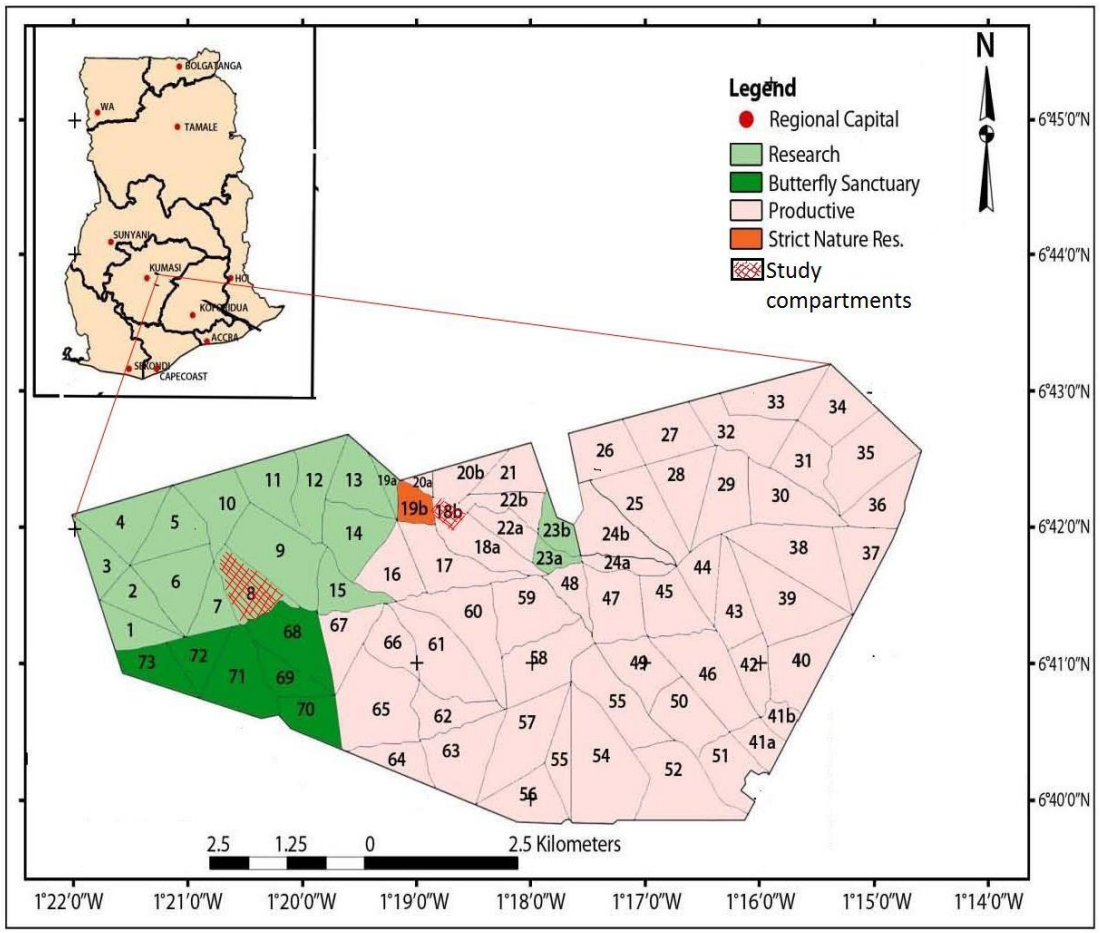


Figure 2: Map of study area (top: map of Ghana showing location of Bobiri Forest Reserve. Bottom: map of Bobiri Forest Reserve showing compartments and selected study compartments.

3.1.2 Vegetation

The reserve is within the Moist Semi-deciduous South East Sub-type forest zone (Hall and Swaine, 1981). Foggie *et al*. (1947) describes the vegetation as a mixed deciduous forest. The forest structure is characterized by very tall canopy, usually 37m in height with some trees occasionally rising as tall as 60m. Standing tall in the upper canopy is a mixture of deciduous and evergreen species essentially occurring in equal proportions (Hall and Swaine, 1981). Prior to logging the reserve was rich in species composition with dominating species being *Celtis* spp. and *Triplochiton scleroxylon.*

3.1.3 Climate

Rainfall pattern experienced at the reserve is bimodal, where the major wet season begins from April through to July, and the minor wet season starts from September through to November. The major dry season follows the minor wet season beginning in December and ending in the middle of March. A shorter dry season occurs in August. Weather data collected for a 10-year period (2003 to 2012) at the campus of Forestry Research Institute of Ghana (FORIG) in Fumesua, a distance of about 21 km from Bobiri Forest Reserve was analysed for the rainfall pattern. The mean annual rainfall ranges from 1210 to 1807 mm (Table 2). The peak mean annual rainfall of 246 mm was recorded in June whereas the month of December recorded the least mean annual rainfall of 24 mm (Table 2).

Table 2: Rainfall data for Bobiri forest reserve collected for a 10-year period (2003–2012) from FORIG weather station (6˚44'N, 1˚30'W).

Months	Years										Average
	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	
Jan	5	11	–	82	28	–	–	–	42.4	12	30.07
Feb	104	40.5	87.55	75.8	95.2	32	130.6	77.4	125.7	30.85	79.96
Mar	56.4	184.5	92.1	92.8	77.7	102.85	122.9	69.3	192.5	111.30	110.24
Apr	143.1	106.2	164.2	98.5	239.2	120.85	116.1	120.7	81.5	185.00	137.54
May	125.1	78.5	207.6	167.6	134.4	210.5	194.5	78.61	59.7	186.20	144.27
Jun	166	77.3	144.7	166	271	313.5	533.7	208.4	331.5	254.20	246.63
Jul	55	157.6	25.35	79	271.3	73	244.9	111.4	152.5	58	122.81
Aug	27.25	136.6	45.75	68.6	107.65	176	20.2	135.6	44.15	3.1	76.49
Sep	203.5	335.3	214	187.4	345.8	182.5	69.7	145	340.1	74.4	209.77
Oct	198.25	226.5	272.5	154	180.2	100.8	112.65	248.8	298.9	203.3	199.59
Nov	155.5	43.25	79.2	69	53.9	16.17	26.31	92.1	32	40	60.74
Dec	6	75.25	1	2.1	2.9	36.2	6.7	34.9	–	52	24.12
Total	1245.1	1472.5	1333.95	1242.8	1807.25	1364.37	1578.26	1322.21	1700.95	1210.36	

Source: Data was obtained from Forestry Research Institute of Ghana

Temperatures are uniformly high with a mean annual maximum temperature of 31.2 ^{o}C (2003 to 2012 data from FORIG). Mean lowest and highest maximum temperatures were 27.4 ^{o}C and 33.8 ^{o}C which occurred in the months of August and February respectively (Table 3).

Table 3: Mean maximum temperature for Bobiri Forest Reserve collected for a 10-year period (2003–2012) from FORIG weather station (6˚44'N, 1˚30'W).

Months	Years										
	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	
Jan	32.9	32.3	31.6	31.9	33.2	32.8	32.6	33.4	31.6	32.8	32.5
Feb	33.9	34.2	33.9	32.4	33.3	34.4	33.4	35.4	32.8	32.7	33.8
											Total
Mar	35.1	33.5	33.0	32.6	34.0	33.1	32.6	34.2	32.6	32.6	33.4
Apr	33.2	32.1	32.7	33.0	31.7	31.5	31.7	31.7	32.4	31.2	32.1
May	32.1	31.1	31.9	30.7	31.1	31.4	31.5	32.0	31.8	30.3	31.4
Jun	30.0	29.9	29.4	30.4	29.5	30.1	30.0	29.1	29.5	28.5	29.6
Jul	28.5	27.7	27.7	28.2	28.7	29.0	28.3	28.3	27.3	27.1	28.1
Aug	28.1	27.4	26.4	27.4	27.2	28.6	27.3	27.9	26.9	27.0	27.4
Sep	29.8	29.8	29.5	29.1	29.5	30.2	29.2	29.1	27.8	39.2	30.4
Oct	31.9	31.2	31.4	30.9	30.5	30.4	31.1	30.7	30.2	30.4	30.9
Nov	32.4	32.3	31.9	31.9	31.1	31.4	31.8	30.9	31.9	32.0	31.8
Dec	31.6	31.5	31.6	32.4	31.9	32.0	32.9	31.7	32.3	40.6	32.9
Total	31.6	31.1	31.0	30.9	30.9	31.2	31.1	31.2	30.6	32.0	31.2

Source: Data was obtained from Forestry Research Institute of Ghana

For the 10-year period, the mean minimum temperature recorded for the area was 22.2 ^{o}C. The highest mean annual minimum temperature of 23.3 ^{o}C occurred for the month of April, whereas the lowest value of 19.9 ^{o}C was recorded in the month of January (Table 4).

Table 4: Mean minimum temperature for Bobiri Forest Reserve collected for a 10-year period (2003–2012) from FORIG weather station (6˚44'N, 1˚30'W).

Months	Years										
	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	
	22.0	21.4	18.1	21.6	18.9	16.8	18.4	22.2	20.9	18.9	
											Total
Jan											19.9
Feb	22.9	21.8	23.2	22.6	23.1	22.2	22.3	22.4	21.8	21.9	22.4
Mar	23.0	22.1	23.0	22.2	23.7	23.0	22.6	23.5	22.5	22.8	22.8
Apr	22.7	23.2	24.0	23.3	23.1	23.9	22.6	23.6	23.2	22.9	23.3
May	23.1	23.1	23.2	22.7	23.0	23.3	22.9	23.5	23.0	22.8	23.1
Jun	22.3	22.3	22.7	22.6	22.6	22.9	22.2	22.9	22.5	22.2	22.5
Jul	21.8	21.4	21.6	22.5	22.3	22.8	21.8	21.7	22.0	21.9	22.0
Aug	21.8	20.9	21.2	22.2	21.8	22.3	22.1	22.0	22.0	21.4	21.8
Sep	22.0	22.2	22.1	22.1	21.9	22.5	22.0	21.8	22.4	22.2	22.1
Oct	22.3	22.3	22.3	22.4	21.8	22.6	22.3	22.6	22.0	22.5	22.3
Nov	22.1	22.6	22.5	21.8	21.9	22.6	22.2	22.2	22.8	22.9	22.4
Dec	20.6	23.0	21.6	20.8	21.2	21.9	22.2	22.2	21.0	22.0	21.6
Total	22.2	22.2	22.1	22.2	22.1	22.2	22.0	22.5	22.2	22.0	22.2

Source: Data was obtained from Forestry Research Institute of Ghana

3.1.4 Compartmentalization

Bobiri Forest Reserve (BFR) was created in 1939 and reserved in its pristine state when it was still an unexploited primary forest (Foggie, 1947; Foli and Pinard, 2009). The forest has been

periodically logged since the 1940's. The reserve covers an area of 5,445 hectares and is divided into 73 compartments. These compartments are further categorized into 4 blocks based on purpose and usage; (1) production (2) research (3) butterfly sanctuary (4) strict nature reserve (Figure 3). The blocks fall under two separate management bodies, namely the Forest Services Division (FSD) and the Forestry Research Institute of Ghana (FORIG). The FSD manages the production block whilst the research, butterfly sanctuary and the strict nature reserve are managed by FORIG.

3.1.5 Study site

The study was conducted in compartment 18b (12-years post-logged site which was a young forest and herein referred to as Y12) and compartment 8 (55-years post-logged site which was an old forest approaching a climax forest; herein referred to as Y55) of the Bobiri Forest Reserve. Respective post logged years are indicative of the number of years since last entry for tree extraction as at 2013. The selected sites are an adjunct of 6 sites from the project, "Does shifting Carbon Use Efficiency determine the growth rates of intact and disturbed tropical forests? Gathering new evidence from African forests". Additionally, these sites form a part of the RAINFOR-GEM forest inventory network (http://gem.tropicalforests.ox.ac.uk). The sites were selected due to the varied years since last entry for logging and are currently being intensively studied, for tree diversity, composition, biomass dynamics, carbon fluxes, soil dynamics, functional traits, and forest dynamics. Characteristics of the sites from unpublished partial data are presented in Table 5.

Table 5: Characteristics of the study sites

History/characteristics	Site	
	Y12	Y55
Compartment number	18b	8
Post-logged years	12	55
Number of entries	2	1
GPS co-ordinates	6.69 N 1.32 W	6.75 N 1.34W
Elevation	279.0	275.5
Tree density	496 trees ha^{-1}	792 trees ha^{-1}
Basal area	27.28 m^2 ha^{-1}	31.14 m^2 ha^{-1}

3.1.5.1 Soil nutrients and belowground Carbon stock

According to Hall and Swaine, (1981), the soil for the entire forest type corresponds to the ochrosol type. The underlying parent material of the reserve is also developed from rock of the Cape Coast Granite series which is deeply weathered (Foggie, 1947). Despite the relative proximity of the two sites, soil analysis (0 to 40 cm depth) undertaken in February 2014 (*Unpublished data; CUE project team*) indicates that the soils at 12-years post-logged site (Y12) and 55-years post-logged site (Y55) differ in terms of fertility (Table 6) and physical properties (Table 7). Effective cation exchange capacity is considerably lower at Y12 (6.32 cmol/kg) than at Y55 site (23.20 cmol/kg). Total exchangeable bases is more than three times higher at Y55 (23.14 cmol/kg) than Y12 site (6.24 cmol/kg) with most of the exchangeable

bases being calcium (cmol/kg) which is also 80 % higher at Y55 (17.89 cmol/kg) than at Y12 site (4.47 cmol/kg). Additionally, available phosphorous is relatively lower at Y12 (6.68 mg/kg) than at Y55 (7.43 mg/kg). Y12 has a higher sand content (49.85 %) than Y55 (35.32 %) site whereas silt is higher for Y55 (55.62 %) than Y12 (46.57 %) site. Carbon concentrations in the soil (0–40cm) of Y12 (1.06 %) are lower than in Y55 (2.53 %) (Table 6). This is mirrored in differences in bulk density, which is greater for Y12 (1.88 g/cm^3) than for Y55 (1.08 g/cm^3) site (Table 7). Similarly total nitrogen content is lower at Y12 (0.12 %) than at Y55 (0.22 %) site. However, soil carbon to nitrogen ratios (C: N) is much higher in Y55 (C: N 11) compared to Y12 (C: N 9).

When converted to carbon stocks, Y55 (95.29 Mg C ha^{-1}) contains more soil carbon than Y12 (71.68 Mg C ha^{-1}) site (Table 8). Additionally, root carbon stock is higher at Y55 (13.23 Mg C ha^{-1}) than at Y12 (7.93 Mg C ha^{-1}) site. However, ground surface litter (GSL) and coarse woody debris (CWD) is higher at Y10 (0.36 Mg C ha^{-1} for GSL; 3.00 Mg C ha^{-1} for CWD) than Y55 (0.38 Mg C ha^{-1} for GSL; 1.95 Mg C ha^{-1} for CWD) site.

Table 6: Soil chemical properties for Y12 and Y55 sites at Bobiri Forest Reserve.

Site	Depth	C	N	C/N	pH	Ca	Mg	K	Na	TEB	(Al+H)	ECEC	BS	P	K
	0—10	1.66	0.16	10.38	6.94	5.61	2.14	0.26	0.1	8.11	0.1	8.21	98.78	6.62	84.43
Y12	10—20	1.44	0.14	10.29	6.89	5.34	1.6	0.26	0.12	7.32	0.1	7.42	98.65	6.54	66.03
	20—30	0.65	0.11	5.91	7.02	4.27	0.8	0.23	0.13	5.43	0.05	5.48	99.09	7.49	51.96
	30—40	0.49	0.05	9.8	7.27	2.67	1.07	0.22	0.15	4.11	0.05	4.16	98.8	6.06	43.66
	Mean ± SD	**1.06 ± 0.58**	**0.12 ± 0.05**	**9.09 ± 2.14**	**7.03 ± 0.17**	**4.47 ± 1.33**	**1.4 ± 0.59**	**0.24 ± 0.02**	**0.13 ± 0.02**	**6.24 ± 1.81**	**0.08 ± 0.03**	**6.32 ± 1.84**	**98.83 ± 0.19**	**6.68 ± 0.60**	**61.52 ± 17.85**
	0—10	4.91	0.37	13.27	7.05	35.78	8.01	0.25	0.12	44.16	0.05	44.21	99.89	5.74	89.48
Y55	10—20	2.4	0.24	10	7.1	16.82	4.27	0.46	0.25	21.8	0.05	21.85	99.77	5.34	84.07
	20—30	1.54	0.15	10.27	7.04	8.81	3.74	0.26	0.12	12.93	0.05	12.98	99.61	8.53	79.02
	30—40	1.26	0.13	9.69	6.9	10.15	3.2	0.21	0.1	13.66	0.1	13.76	99.27	10.13	84.07
	Mean ± SD	**2.53 ± 1.66**	**0.22 ± 0.11**	**10.81 ± 1.66**	**7.02 ± 0.09**	**17.89 ± 12.43**	**4.81 ± 2.18**	**0.3 ± 0.11**	**0.15 ± 0.07**	**23.14 ± 14.58**	**0.06 ± 0.023**	**23.2 ± 14.57**	**99.64 ± 0.27**	**7.43 ± 2.29**	**84.16 ± 4.27**

Ca, Mg, K, Na-excheangeable calcium, magnesium, potassium and sodium; TEB, total exchangeable bases; Al+H, exchangeable acidity; ECEC, effective cation exchange capacity (all in cmol/kg); C, N, BS- total carbon, nitrogen and base saturation (all in

%); P, K-available phosphorus and potassium (all in mg/kg). Data was obtained from studies in 2014 by CUE project team 31

Table 7: Soil physical properties for Y12 and Y55 sites at Bobiri Forest Reserve.

Site	Depth	Sand (%)	Clay (%)	Silt (%)	Bulk Density (g/m3)	Texture
Y12	0—10	54.1	4.03	41.87	1.42	Sandy loam
	10—20	47.04	4.12	48.84	1.54	Sandy loam
	20—30	46.66	2.09	51.25	2.3	Silty loam
	30—40	51.6	4.07	44.33	2.25	Sandy loam
	Mean	**49.85 ± 3.61**	**3.58 ± 0.99**	**46.57 ± 4.25**	**1.88 ± 0.46**	
Y55	0—10	40.06	6.1	53.84	0.63	Silty loam
	10—20	35.5	6.04	58.46	1.24	Silty loam
	20—30	34.82	6.08	59.1	1.34	Silty loam
	30—40	30.9	18.04	51.06	1.13	Silty loam
	Mean	**35.32 ± 3.75**	**9.07 ± 5.98**	**55.62 ± 3.84**	**1.08 ± 0.32**	

Data was obtained from studies in 2014 by CUE project team

Table 8: Carbon stock (Mg C ha^{-1}) estimates for Y12 and Y55 sites at Bobiri Forest Reserve.

Carbon stocks	Depth (cm)	Site	
		Y12	Y55
Soil	0—10	23.56	30.81
	10—20	22.14	29.69
	20—30	14.93	20.57
	30—40	11.05	14.21
	Total	**71.68**	**95.29**
Roots*	0—30	7.93	13.23
Surface litter#	—	0.36	0.28
Coarse woody debris#	—	3	1.95

*Data was obtained from studies in 2012 by CUE project team; # Data was obtained from Boakye (2014).

3.2 Period of study

The respiration, (soil respiration and respiration from component contributions) and climate (soil temperature, soil moisture, rainfall and air temperature) at both sites were measured monthly from May 2013 to April 2014.

3.3 Experimental design

In each study compartment, 1.0 hectare (ha) square plots were established with a tree stump that was felled during the last entry (logging) as the center of the plot. Each main plot was divided into 25 subplots of dimension 20 m $\times$ 20 m (400 m^{-2}) forming a sampling grid and serving as sampling points for the various measurements. The subplots served as a basis for replication for total soil respiration measurements (Metcalfe *et al.*, 2008b; Fenn *et al.*, 2010). In addition, nine spots were systematically selected at the four corners of the main plot, at the mid sections (i.e. 50 m from the corners of the plot along the boundaries) and at the centre of the plot. These points also served as points for respiration partitioning experiment (the set-up is further expatiated in the proceeding section). Schematic presentation of the sample plot design is given in Figure 3.

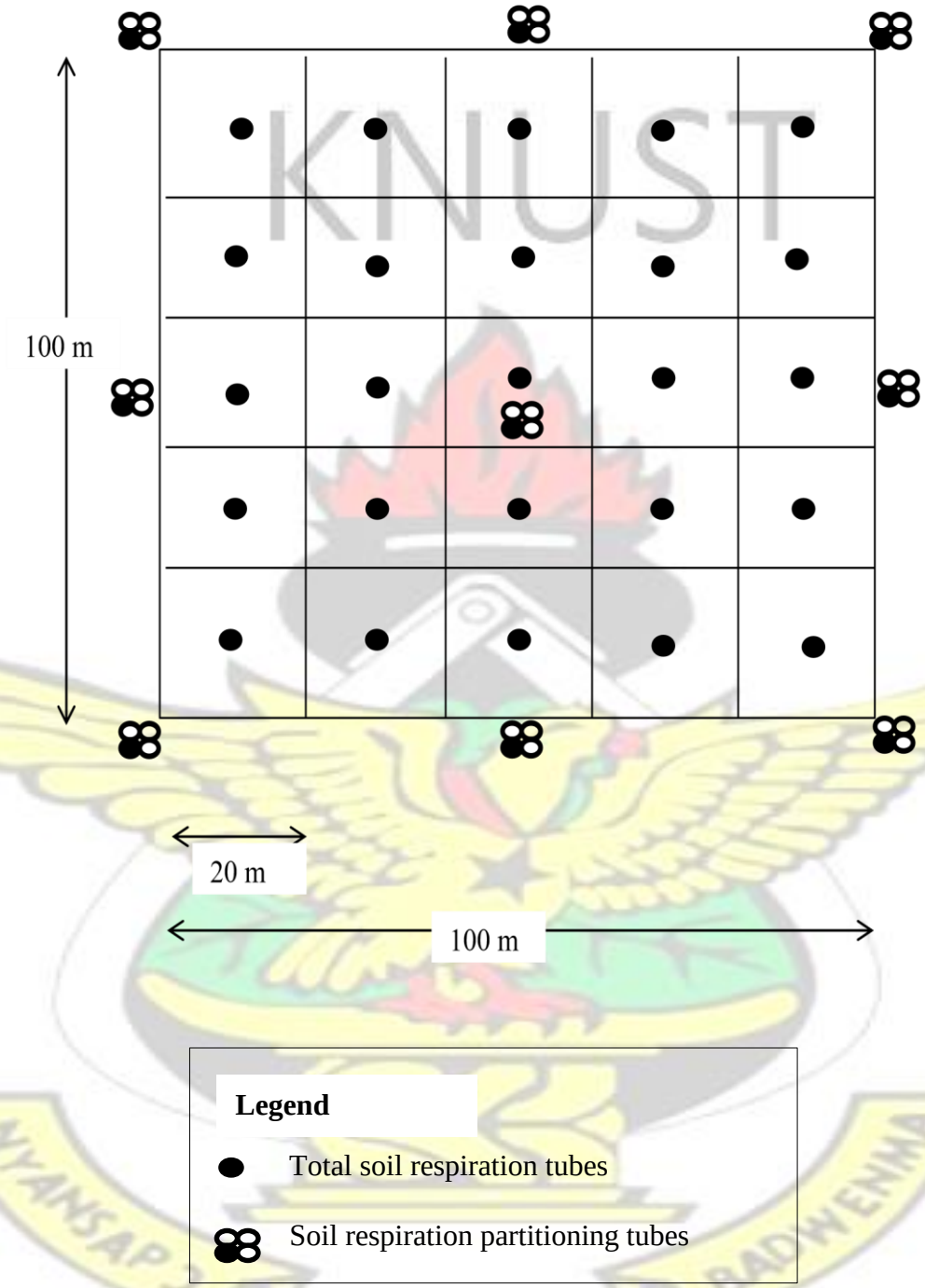


Figure 3: Schematic presentation of the sample plot design.

3.4 Study installations and data collection

3.4.1 Total soil respiration

Soil collars (made from ~ 13cm diameter and 10 cm length PVC tubes) were installed in each of the 25 subplots, approximately in the center of the subplot and at the 9 points as aforementioned in the preceding section. Each collar was installed to a depth of 5 cm into the soil, leaving 5 cm aboveground to provide fixed points for soil respiration measurements while minimizing soil and root disturbance. Collars were left in place for over 8 months before the first measurements were carried out.

Soil CO_2 efflux measurement was carried out at monthly intervals at all 34 sampling points. The measurements were carried out by means of an Infrared Gas Analyzer (IRGA) (EGM-4; PP Systems, Hitchin, U.K.) and soil respiration chamber (SRC) (SRC-1; PP Systems, Hitchin, U.K.) (Plate 1a). The SRC was modified with a custom-made adaptor to fit the tubes. The measuring principle is a closed system that determines the increase in CO_2 concentration within the chamber headspace over a period of 124 seconds. The short period of 124 seconds is to avoid high accumulation of CO_2 in the chamber which can impact on the CO_2 efflux.

3.4.2 Soil temperature and soil moisture

After each CO_2 measurement, soil temperature and moisture were measured in the same soil collar and at four locations around the collar to a depth of 5 cm using a temperature (Digital Waterproof Thermometer, Barnstead International, Dubuque, USA) and moisture probe (Hydrosense meter, Campbell Scientific, Australia) respectively (Plate 1b).

Plate 1: Measurement of soil respiration and soil variables. (a) Measuring soil respiration using the Infrared gas analyzer system; (b) measuring soil temperature using a soil temperature probe.

3.4.3 Partitioning components of soil respiration

Soil respiration was partitioned into separate contributions using a combination of surface and deep collars to enclose a core of soil in situ, from which soil respiration measurements were periodically taken. The partitioning experiment (Figure 4; Plate 3) consisted of a group of 4 collars (PVC tubes; i.e. 2 tubes of 10 cm, and 2 tubes of 40 cm). Each group consisted of the following treatments (Figure 4; Plate 3):

1. CONTROL;

The control collar was one of total soil respiration collars aforementioned. It was a 10 cm PVC tube which was pressed 5cm into the soil, leaving 5 cm aboveground to ensure an air tight seal whilst minimizing root disturbance. Since there were no manipulations made to this collar, the control collar consisted of all soil components namely litter, roots-and-rhizosphere (the

rhizosphere is the region of soil influenced by the root system, i.e. where the microbial population is affected by nutrient uptake and release of compounds by the root), mycorrhizae and soil organic matter (SOM). This could be written mathematically as:

$$\text{Control} = \text{Litter} + \text{Roots and rhizosphere} + \text{Mycorrhizae} \quad (1)$$

2. NL (No Litter);

The NL collar was also a 10 cm PVC which was pressed 5cm into the soil to ensure an air tight seal whilst minimizing root disturbance. However aboveground surface litter was removed and gravels were placed on surface of the soil within the collar to exclude future litter inputs (Plate 3). Therefore the NL collar consisted of only roots, mycorrhizae and soil organic matter (SOM). This can be written mathematically as:

$$\text{NL} = \text{Roots and rhizosphere} + \text{Mycorrhizae} + \text{SOM} \quad (2)$$

3. NLR (No Litter, Roots);

The NLR collar was also a 40 cm PVC which was inserted deep into the soil. Prior to insertion, two pairs of openings (windows) (that is 3.5 cm diameter holes) were created at the opposite sides of the tube. The windows in a pair were separated by a distance of 5 cm. The windows were covered with fine 41µm gauge nylon mesh (Plate 2B). This was done to exclude lateral root ingrowth but permit ingrowth of mycorrhizal hyphae. A deep soil core was then dug and roots were manually removed after which the tube was inserted into the ground and backfilled with the root-free soil (Plate 2A, C and D). After installation, surface litter was removed and gravels were placed on surface of the soil within the collar to exclude future litter inputs (Plate 3). Hence the NLR collar consisted of only mycorrhizae and soil organic matter (SOM). This can be written mathematically as:

NLR = Mycorrhizae +

SOM

(3)

4. NLRM (No Litter, Roots, Mycorrhizae);

The NLRM collar was also a 40 cm PVC which was inserted deep into the soil similar to the NLR collar above. However, no windows were created on the tubes. Hence this excluded lateral ingrowth of both roots and mycorrhizal hyphae. A deep soil core was then dug and roots were manually removed after which the tube was inserted into the ground and backfilled with the root-free soil. After installation, surface litter was removed and gravels were placed on surface of the soil within the collar to exclude future litter inputs (Plate 3). Hence the NLRM collar consisted of only soil organic matter (SOM). This can be written mathematically as:

NLRM =
SOM

(4)

Within a group, each tube was installed 50cm from the centers of each other (Plate 3) while each group of tubes was placed at 50 m from each other (Figure 3). Groups were installed at nine locations (secondary subplots) as a basis of replication and this included the four corners of the plot edges, the middle of each 100 m side (every 50 m) and one group at the center of the plot (Figure 3). Soil respiration measurements were recorded monthly at the sampling points using an Infrared Gas Analyzer (IRGA) (EGM-4; PP Systems, Hitchin, U.K.) and soil respiration chamber (SRC) (SRC-1; PP Systems, Hitchin, U.K.) as described above.

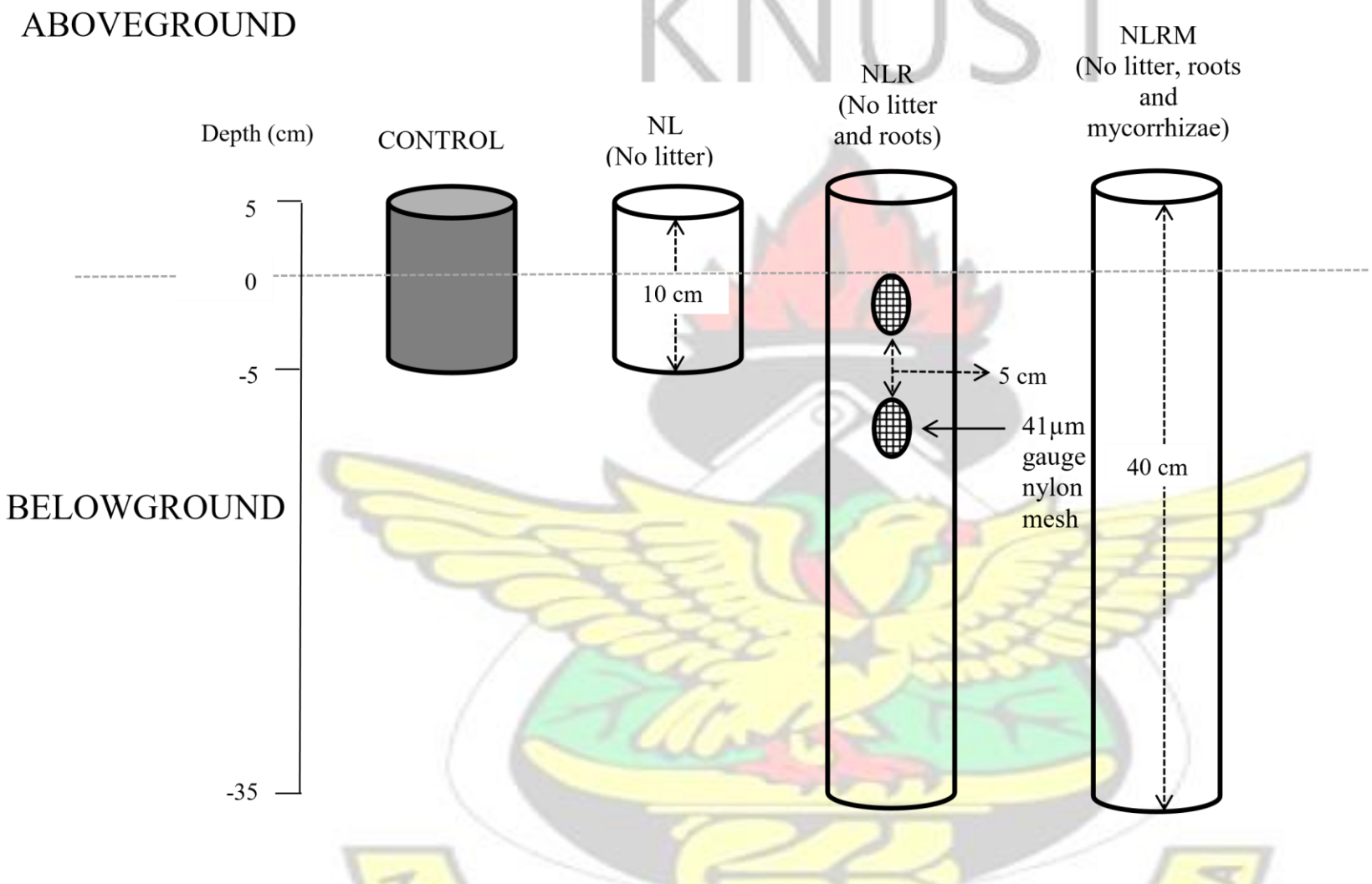


Figure 4: Experimental set-up utilized for partitioning total soil respiration.

Plate 2: Installation of respiration partitioning experiment. (A) Removal of roots from dugout soil core; (B) 40 cm tube with fine 41µm gauge nylon mesh windows that exclude roots but permits ingrowth of mycorrhizal hyphae; (C) Inserting PVC tube into soil; (D) Backfilling inserted PVC tube with root-free soil.

Plate 3: Installed respiration partitioning experiment. Gravels were placed in NL (no litter), NLR (no litter and roots) and NLRM (no litter, roots and mycorrhizae) collars to exclude litter accumulation.

3.5 Measurement of meteorological data

Precipitation and daily air temperature data from a nearby weather station at the campus of the Forestry Research Institute of Ghana (FORIG) (6˚44'N, 1˚30'W), located 21 km from the site

was utilized. Precipitation was measured with a rain gauge while air temperature was measured with a thermometer placed in a Stevenson screen.

3.6 Data processing and analyses

3.6.1 Soil Respiration

Each CO_2 measurement was quality controlled with the CO_2 concentration in the soil respiration chamber headspace linearly related to time. This could be represented by the equation:

$$y = mx + c \quad (5)$$

Where

"y" is the CO_2 concentration (ppm),

"m" is the slope which represents the rate of change in CO_2 with time "x" (ppm s^{-1}) and

"c", the intercept on the y axis is a measure of the initial CO_2 concentration in the chamber.

Appendix 1A and 1B show examples of the derived relationship from selected months over the study period and the rate of change in CO_2 with time for each month respectively. Also atmospheric pressure was measured by the Infra-red Gas Analyser during each measurement. Monthly values are presented in Appendix 1C.

Each soil respiration rate was then calculated from the rate of change of CO_2 concentration within the soil respiration chamber headspace, the atmospheric pressure, soil temperature measured with the soil temperature probe and the chamber volume. Soil respiration was then calculated as (*cf.* Metcalfe *et al.,* 2007):

$$r_s = \frac{\Delta C}{\Delta t} \times \frac{P}{1000} \times \frac{273}{(T+273)} \times \frac{44.01}{22.41} \times \frac{Vch}{\mathrm{A}} \times \frac{1}{1000} \times \frac{1}{3600} \quad (6)$$

Where

r_s; Soil respiration rate (g CO_2 m^{-2} hr^{-1}),

ΔC/Δt; Rate of change in CO_2 within the SRC chamber (ppm s^{-1}),

P; Atmospheric pressure (Pa),

T; Soil temperature (^OC),

Vch; Total internal volume of the SRC plus volume of PVC collar (m^3) and

A; Ground area covered by the chamber (m^2).

The division by 1000 and subsequent multiplication by 3600 was to convert r_s from units of kg m^{-2} s^{-1} to g m^{-2} hr^{-1}.

3.6.2 Soil respiration partitioning

Total soil respiration is a combination of respiration from components of surface organic litter (Rlitter), root and rhizosphere (Rr,rhizo), mycorrhizae (Rmyc) and soil organic matter decomposition (Rsom) which could be written mathematically as:

Rs = Rlitter + Rr, rhizo + Rmyc + Rsom (7) Hence with reference to equations (1), (2), (3) and (4), respiration from the various components was calculated as follows:

- Litter respiration (Rlitter) = Control − NL (8)
- Root and rhizosphere respiration (Rr, rhizo) = NL − NLR (9)
- Mycorrhizal respiration (Rmyc) = NLR −

NLRM (10)

- SOM respiration (Rsom) =

NLRM (11)

Autotrophic respiration was taken as the combination of root-and-rhizosphere respiration and mycorrhizal respiration whereas heterotrophic component was taken as respiration from litter, and SOM decomposition.

3.6.3 Annual and seasonal respiration estimates

Annual site respiration for total soil and each component was estimated by summing the monthly day-time fluxes for the year. This was calculated as:

$$R_{asc,i} = \sum_{j=1}^{12} \left(r_s \times 10^{-6} \times A \times \frac{12}{44} \times 730.5 \right)(j) \qquad (13)$$

Where:

$R_{asc,i}$; Annual soil respiration rate from soil or soil component at site, *i* (Mg C ha^{-1} yr^{-1})

r_s; Total soil or component respiration rate at site, i of the j-th month (g CO_2 m^{-2} hr^{-1})

A; Area of site *I* (ha)

12; Relative molar mass of carbon (C)

44; Relative molar mass of carbon dioxide (CO_2)

730.5; Average number of hours in a month

The value 10^{-6} converts from units of g to Mg. Also, since there are 365.242 days in a year, multiplying this by 24 hours and then dividing by 12 gives 730.5 hours which is the average number of hours in a month. Therefore, the value 730.5 converts daily fluxes to monthly fluxes.

To compare the average soil respiration in each season, soil respiration was grouped by months following the rainfall pattern where fluxes occurring in months with rainfall less than 100 mm (August, December, January, February and March) classified as dry season respiration and fluxes in months greater than 100 mm (May, June, July, September, October, November and April) classified as wet season respiration. This was calculated as:

$$R_{ssc,i} = \frac{1}{n}\sum_{i=1}^{n} R_{msc,i} \quad (14)$$

Where;

$R_{ssc,i}$; Average seasonal respiration from soil or soil component at site, *i* (g CO_2 m^{-2} hr^{-1})

$R_{msc,i}$; Monthly average respiration from soil or soil component at site, *i* (g CO_2 m^{-2} hr^{-1}) *n;* Number of months within a particular season.

3.7 Statistical Analysis

Student's *t*-test statistic was used to assess mean monthly and annual differences in total soil respiration, soil component respiration and climatic variables between the two sites. The spatial variability in soil respiration and climatic variables was expressed using the coefficient of variation (CV) calculated as:

$$CV = \frac{\text{Standard Deviation}}{\text{Mean}} \times 100\ \% \quad (15)$$

To test for significant seasonal changes in total soil respiration, soil component respiration and climatic variables for each site, repeated measures analysis of variance (RMANOVA) was used. Also, one-way analysis of variance was also used to assess differences in annual respiration estimates within sites. Both linear and non-linear regression analyses were used to test the relationship between soil respiration (Rs) soil temperature (T) and soil moisture (M). Significant differences for all statistical tests were evaluated at the level α=0.05. Analyses were performed using SPSS for Windows (SPSS Inc.) and results were displayed in tables and graphs using Microsoft Excel (Microsoft Corporation).

CHAPTER FOUR

4.0 RESULTS

4.1 Ancillary climate data

4.1.1 Rainfall and daily air temperature

Monthly climate data measured for the study period are presented in Appendix 2. The climate was characterized by a strong seasonality in rainfall depicting a typical bimodal pattern (Figure

5a). A major peak occurred in the month of September (~457.1 mm) during the minor wet season (September-November). The dry periods with rainfall below 100 mm occurred in 5 months i.e. August (minor dry season) and December through to March (major dry season). Rainfall was lowest during the month of December (~10 mm) with approximately 3 rainy days. In all, the annual total rainfall for the study period was approximately 1709.60 mm (Appendix 2). This was 281.82 mm higher when compared to the long-term annual average rainfall of 1427.78 mm recorded from 2003 to 2012 for the study area (Table 2).

The mean annual maximum air temperature was approximately 30.04 °C for the study period (Appendix 2). Maximum air temperature at the start of the study declined till July recording its lowest (32.58 °C), and then rose steadily being fairly constant throughout the rest of the study period (Figure 5b). Monthly mean maximum air temperature occurred in July at a value of 26.15 °C. On the other hand, mean annual minimum air temperature was 22.38 °C (Appendix 2). Minimum temperature was fairly constant throughout the study period exhibiting a major dip in December 20.36 °C (Figure 5c). Monthly minimum air temperature peaked in April at a value of 23.67 °C.

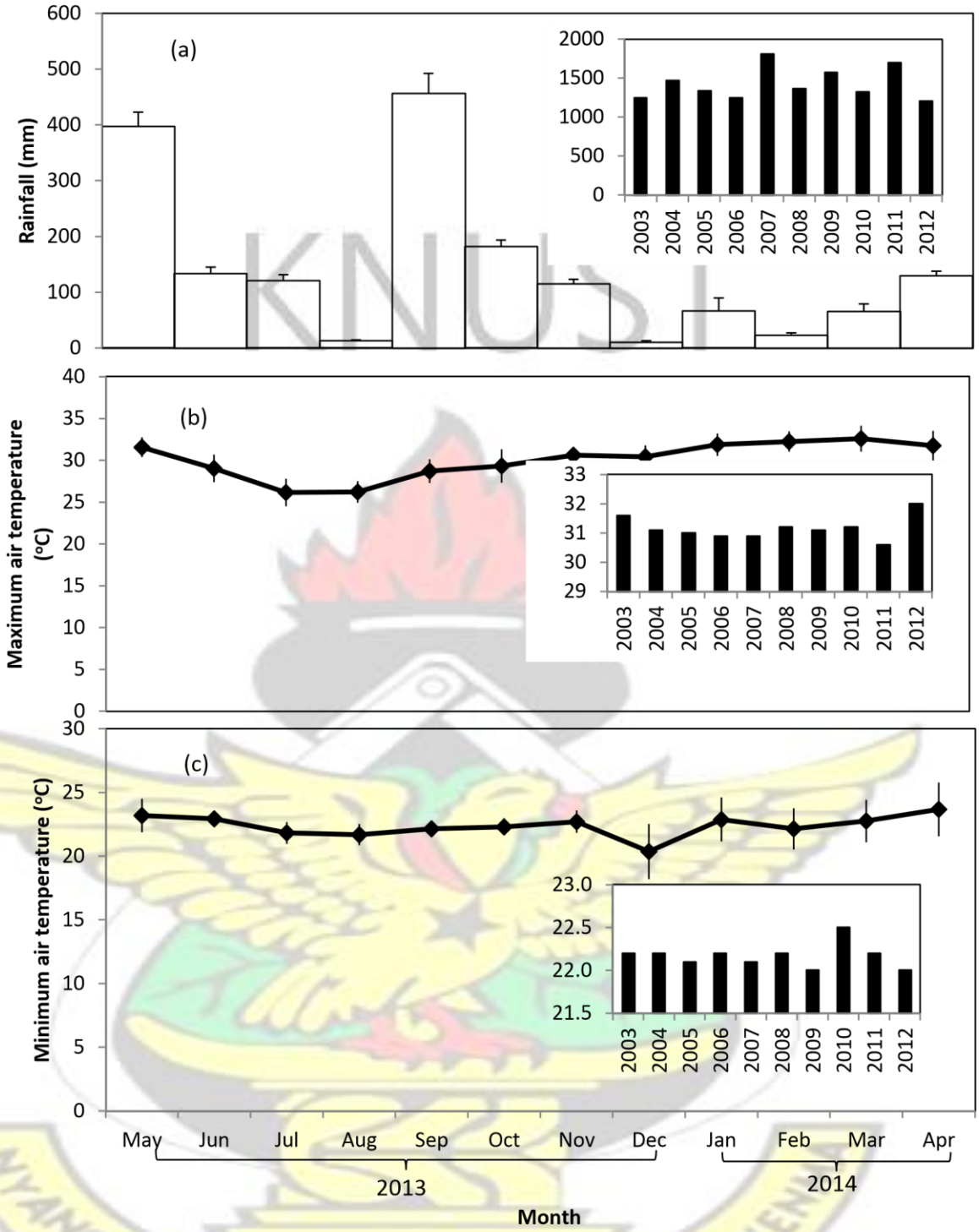
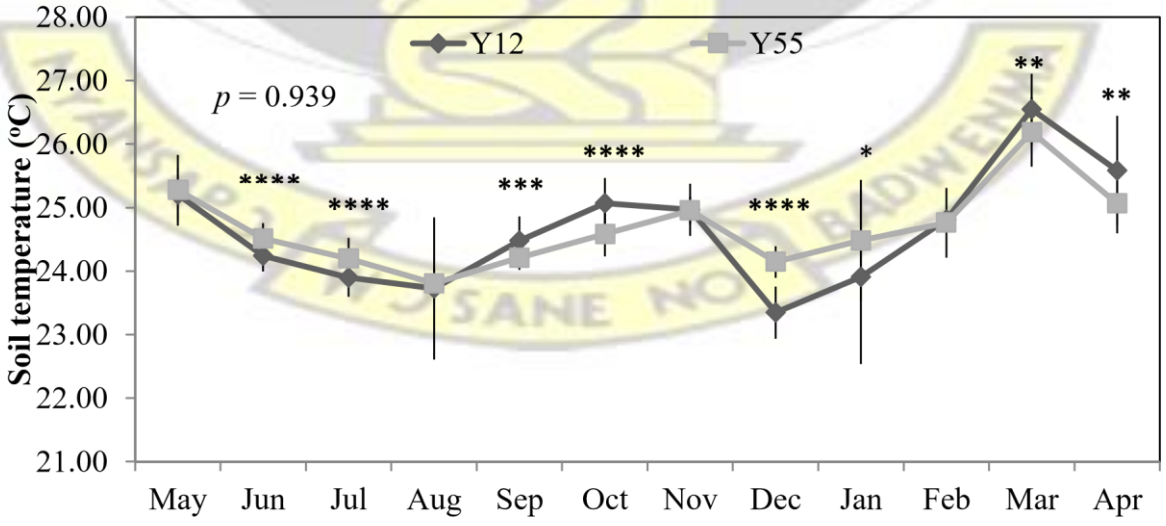


Figure 5: Climate data for Seasonal (main) and annual (insert), (a) rainfall, (b) maximum temperature and (c) minimum air temperature measured for the study area. Data were obtained from FORIG weather station (6˚44'N, 1˚30'W). Error bars represent standard deviations.

4.2 Soil temperature and soil moisture

Day-time averages of soil temperature and soil moisture measured monthly from 34 locations at both sites are presented in Figure 6 and in Appendix 3A and 3B respectively. No significant difference in mean annual temperature was found between both sites (*t*-test, $p > 0.05$) for either soil temperature or soil moisture. At both sites, coefficient of variation (CV) for soil moisture (annual mean, 47.23 % at Y12 site and 34.39 % at Y55 site) was higher than soil temperature (annual mean, 2.29 % at Y12 site and 1.67 % at Y55 site). This suggests a higher spatial variation in soil moisture than temperature.

The temporal variation in soil temperature showed similar tendency in both sites whereby soil temperature was high at the start of the measurement period in May but was observed to decline and show a similar dip in August and December at both sites (Figure 6). The peak in soil temperature occurred in March at a value of 26.55 ± 0.56 SD ^{o}C and 26.19 ± 0.55 ^{o}C at Y12 and Y55 site respectively. Also, soil moisture exhibited a clear pattern with the highest peak for both sites occurring in October (10.64 ± 3.38 % at Y12 and 10.10 ± 2.13 at Y55 site), the month following peak rainfall and the lowest occurring in January (2.95 ± 0.96 %) and August (2.72 ± 1.12 %) at Y12 and Y55 site respectively (Figure 6).



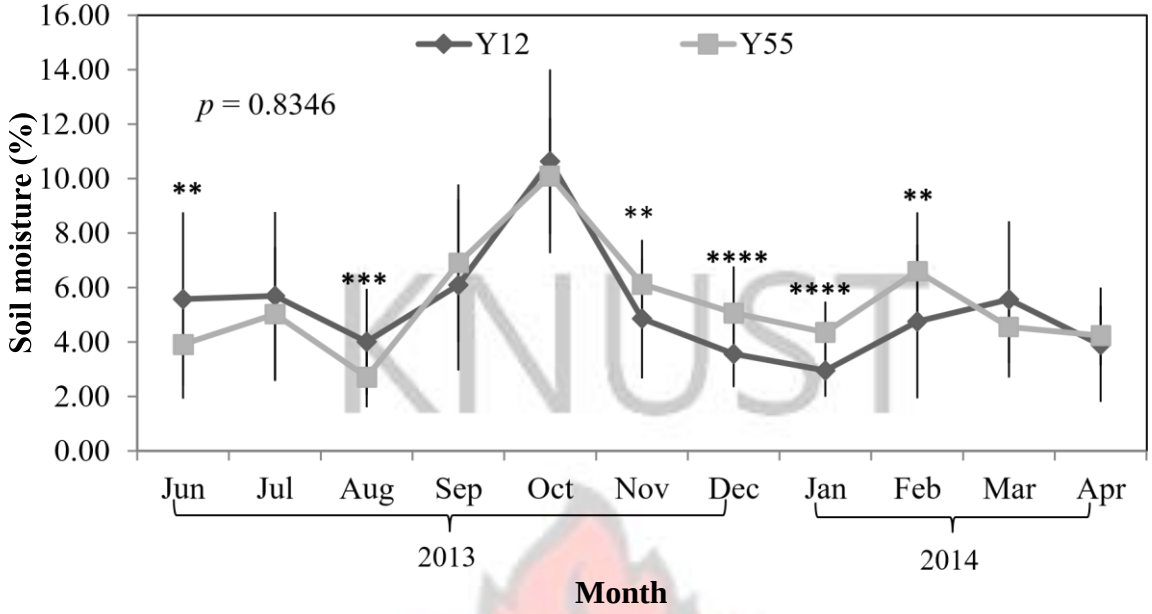


Figure 6: Monthly variation in soil temperature (upper panel) and soil moisture (lower panel) for Y12 and Y55 site measured over the study period. The *p* – value denotes significant level between sites tested for the entire study period using Student's *t*-test. Significant difference within the corresponding month is denoted by asterisk: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$ (Student's *t*-test). Error bars represent standard deviation.

In terms of seasonality, soil temperature during the wet season was significantly higher ($p < 0.0001$; Table 9; Appendix 3E) than dry season soil temperature at Y12 site. At Y55 site, wet season soil temperature was also higher than dry season but no significant difference was observed ($p > 0.05$; Table 9; Appendix 3E). Soil moisture during the wet season was significantly higher ($p < 0.0001$; Table 9; Appendix 3E) than average dry season soil moisture at both sites.

Table 9: Seasonal estimates of soil temperature (º C) and soil moisture (%) for Y12 and Y55 site

Site	Season	Soil temperature (º C)		Soil moisture (%)	
		Mean (±SD)	CV (%)	Mean (±SD)	CV (%)
Y12	Wet	24.73 (0.26)	1.06	6.13 (1.78)	29.11
	Dry	24.47 (0.34)	1.38	4.17 (1.50)	35.96
	p - value	< 0.0001		< 0.0001	
Y55	Wet	24.70 (0.20)	0.79	6.03 (1.30)	21.6
	Dry	24.68 (0.28)	1.14	4.66 (1.01)	21.67
	p - value	0.655		< 0.0001	

Values are results from monthly averages, SD is standard deviations, and CV is coefficient of variation. *P*-values denote significance level from repeated measures ANOVA.

4.2.1 Soil temperature and soil moisture in partitioning tubes

Monthly averages of day-time soil temperature and soil moisture within partitioning collars at both sites are shown in Appendix 3C and 3D. The pattern of seasonal variation for either soil temperature or soil moisture was similar across the four partitioning treatments (Figure 7). Although a one-way analysis of variance (ANOVA) test for collar differences in soil temperature at each site revealed a significant collar difference during the month of February at Y55 site, ANOVA for the entire study period using pooled data was not significant ($p > 0.05$) for both soil temperature and soil moisture at both sites.

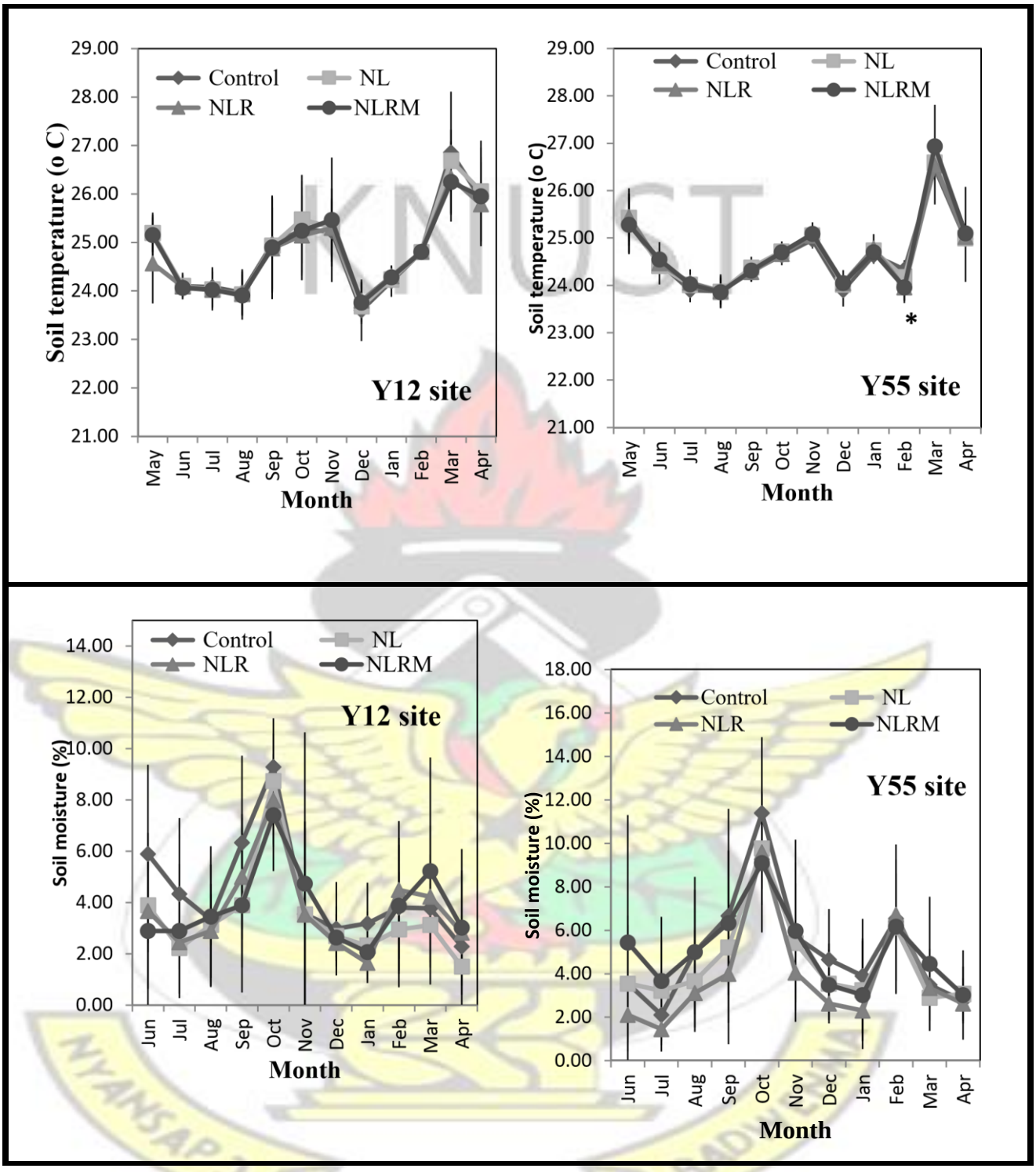


Figure 7: Monthly variation in soil temperature (upper panel) and soil moisture (lower panel) from soil respiration partitioning collars for Y12 and Y55 site measured over the study period. Collars denote: Control; NL-no litter; NLR- no litter and roots; NLRM- no litter, roots and mycorrhizae. Error bars represent standard deviation.

4.3 Total soil respiration

4.3.1 Seasonal variation

Monthly averages of total soil respiration at both sites are shown in Appendix 4A. No significant difference in total soil respiration for the entire study period was found between both sites (*t*-test, $p > 0.05$). However, Student's *t*-test paired for each month showed soil respiration to be significantly different between sites in four out of the twelve months studied depicting that each month's respiration was dependent on site. The coefficient of variation (CV) for soil respiration was higher at the 55-years post-logged site (Y55) (annual mean, 52.22 %) than 12-years post-logged site (Y12) (47.94 %). The higher CV for Y55 suggests a greater spatial variation in soil respiration than Y12 site.

Temporally, total soil respiration at both sites exhibited a strong seasonal cycle (Figure 8) where respiration generally increased during the wet periods and decreased during the dry periods, corresponding to the seasonal changes of rainfall and soil moisture (Figure 5a and Figure 6). At Y12 site, soil respiration decreased till August and thereafter increased in September to October. Soil respiration rate decreased in November recording consistently low rates throughout the major dry season (December to March). A similar pattern was observed at Y55 site although soil respiration depressed in May.

At both sites, average soil respiration during the wet season was significantly higher ($p < 0.0001$; Appendix 4D) than average dry season respiration. Average soil respiration at Y12 site during the wet and dry season were 0.84 ± 0.22 g CO_2 m^{-2} hr^{-1} and 0.55 ± 0.18 g CO_2 m^{-2} hr^{-1} which corresponds to percentages of 60.29 % and 39.71 % respectively of total annual site respiration (Table 10). At Y55 site, average wet and dry season respiration were 0.80 ±

0.22 g CO_2 m^{-2} hr^{-1} and 0.68 ± 0.35 g CO_2 m^{-2} hr^{-1} corresponding to percentages of 54.15 % and 45.85 % respectively of total annual site respiration respectively. Also the coefficient of variation (CV) in soil respiration was higher in dry season (32.86 % for Y12 and 51.35 % for Y55) than wet season (26.27 % for Y12 and 27.81 % for Y55) for both sites.

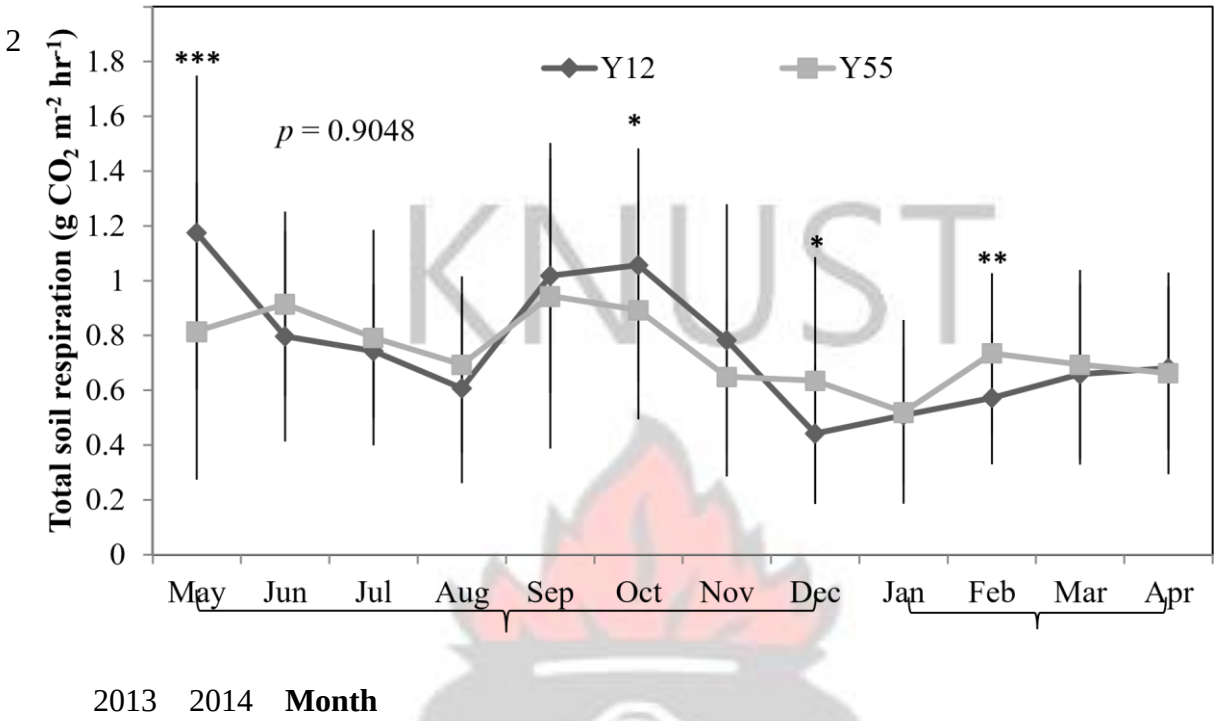


Figure 8: Monthly variation in total soil respiration for Y12 and Y55 measured over the study period. The *p* – value denotes significant level between sites tested for the entire study period using Student's *t*-test. Significant difference within the corresponding month is denoted by asterisk: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ (Student's *t*-test). Error bars represent standard deviation.

Table 10: Seasonal estimates of total soil respiration (g CO_2 m^{-2} hr^{-1}) for Y12 and Y55 site

Site	Season	Mean (±SD)	Percentage (%)	CV (%)
	Wet	0.84 (0.22)	60.29	26.27
Y12	Dry	0.55 (0.18)	39.71	32.86
	p - value	< 0.0001		
	Wet	0.80 (0.22)	54.15	27.81
Y55	Dry	0.68 (0.35)	45.85	51.35
	p - value	0.003		

Values are results from monthly averages, SD is standard deviations, and CV is coefficient of variation. *P*-values denote significance level from repeated measures ANOVA.

4.4 Components of soil respiration

4.4.1 Partitioning treatments

Monthly averages of soil respiration for the different partitioning collars at both sites are shown in Appendix 4B. The soil respiration measured over the study period showed clear differences between partitioning tubes with CO_2 flux rates generally decreasing in the treatment order CONTROL > NL > NLR > NLRM at both sites (Figure 9). A one-way analysis of variance (ANOVA) test for the entire study period using pooled data indicated significant differences between partitioning collars ($p < 0.0001$) at both sites. This suggests a successful partitioning of soil respiration at both sites.

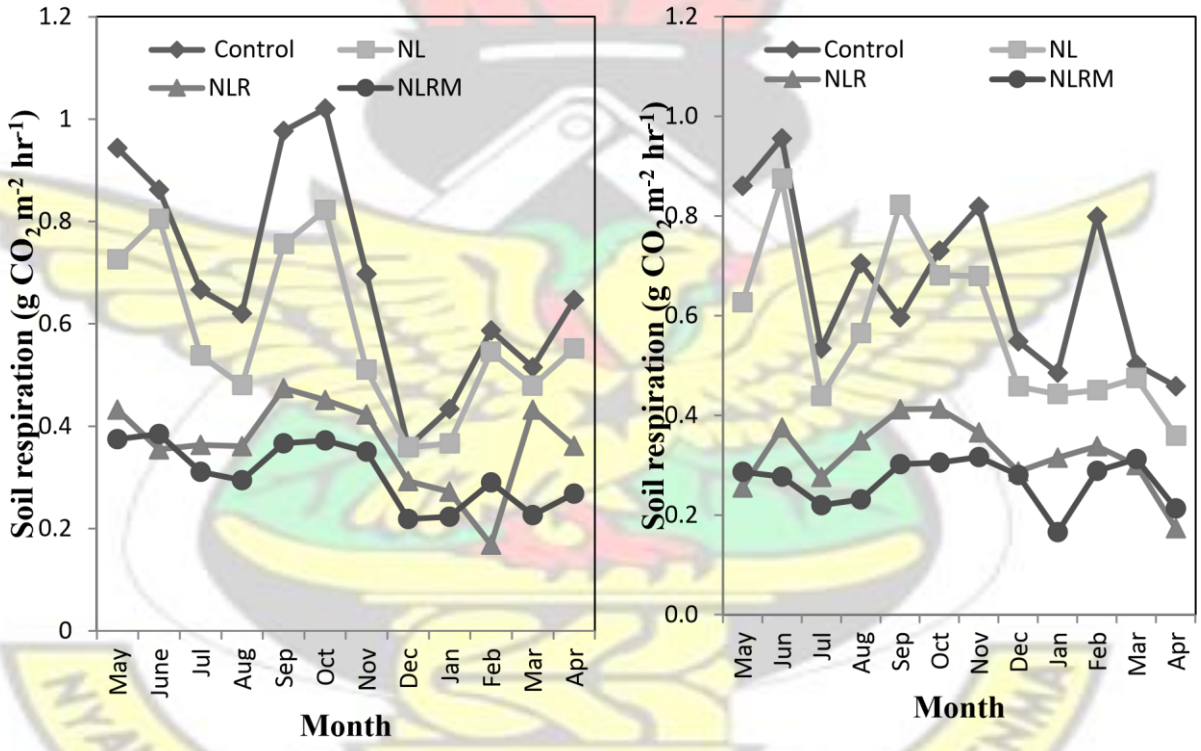


Figure 9: Monthly variation in soil respiration from partitioning collars for Y12 (left panel) and Y55 (right panel) site measured over the study period. Collars denote: Control; NL-no litter; NLR- no litter and roots; NLRM- no litter, roots and mycorrhizae.

4.4.2 Root-and-rhizosphere respiration

Monthly averages of root-and-rhizosphere respiration at both sites are shown in Appendix 4C. No significant difference in root-and-rhizosphere respiration for the entire study period was

found between both sites (*t*-test, $p > 0.05$) although Student's *t*-test for each month showed root-and-rhizosphere respiration to be significantly lower at Y12 site during the month of December (Figure 10; Appendix 4C). Seasonally, the root-and-rhizosphere respiration at both sites exhibited a similar and strong pattern whereby the root-andrhizosphere respiration generally increased during the wet periods and decreased during the dry periods (Figure 10).

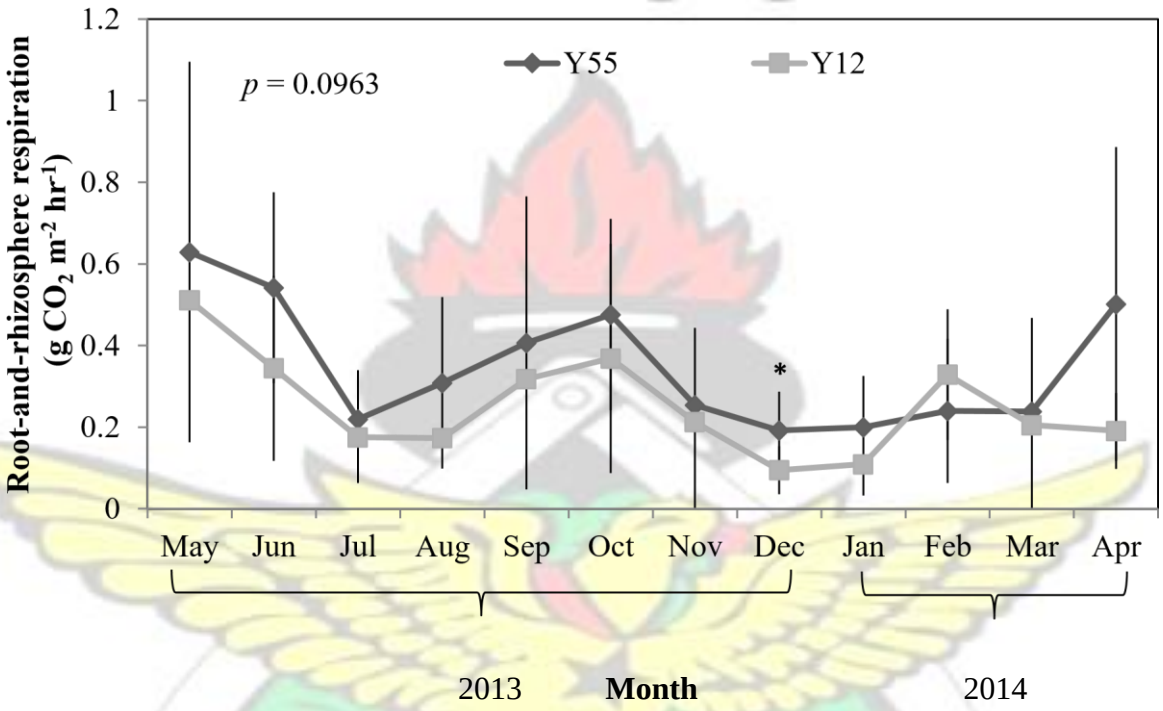


Figure 10: Monthly variation in root-and-rhizosphere respiration for Y12 and Y55 measured over the study period. The *p* – value denotes significant level between sites tested for the entire study period using Student's *t*-test. Significant difference within the corresponding month is denoted by asterisk: * $p < 0.05$ (Student's *t*-test). Error bars represent standard deviation.

At both sites, average root-and-rhizosphere respiration during the wet season was significantly higher (Y12, $p = 0.0026$; Y55, $p = 0.0046$; Appendix 4D) than dry season respiration. Average root-and-rhizosphere respiration at Y12 site during the wet and dry season were 0.28 ± 0.10 SD g CO_2 m^{-2} hr^{-1} and 0.14 ± 0.07 g CO_2 m^{-2} hr^{-1} respectively (Table 11). At Y55 site, average wet and dry season root-and-rhizosphere respiration were 0.40 ± 0.15 g CO_2 m^{-2} hr^{-1} and 0.21

±0.14 g CO_2 m^{-2} hr^{-1} respectively. Furthermore, the coefficient of variation (CV) in root-and-rhizosphere respiration was higher in dry season than wet season at both sites (Table 11).

Table 11: Seasonal estimates of root-and-rhizosphere respiration (g CO_2 m^{-2} hr^{-1}) for Y12 and Y55 site

Site	Season	Mean (±SD)	CV (%)
Y12	Wet	0.28 (0.10)	36.51
	Dry	0.14 (0.07)	46.53
	p - value	0.0026	
Y55	Wet	0.40 (0.15)	37.55
	Dry	0.21(0.14)	66.85
	p - value	0.0046	

Values are results from monthly averages, SD is standard deviations, and CV is coefficient of variation. *P*-values denote significance level from repeated measures ANOVA.

4.4.3 Mycorrhizal respiration

Monthly averages of mycorrhizal respiration at both sites are shown in Appendix 4C. No significant difference in mycorrhizal respiration for the entire study period was found between both sites (*t*-test, $p > 0.05$). However, Student's *t*-test for each month showed mycorrhizal respiration to be significantly lower at Y55 site during May. Similarly significantly lower values were observed at Y12 site during January and April. Temporally, mycorrhizal respiration did not show any clear pattern at both sites (Figure 11).

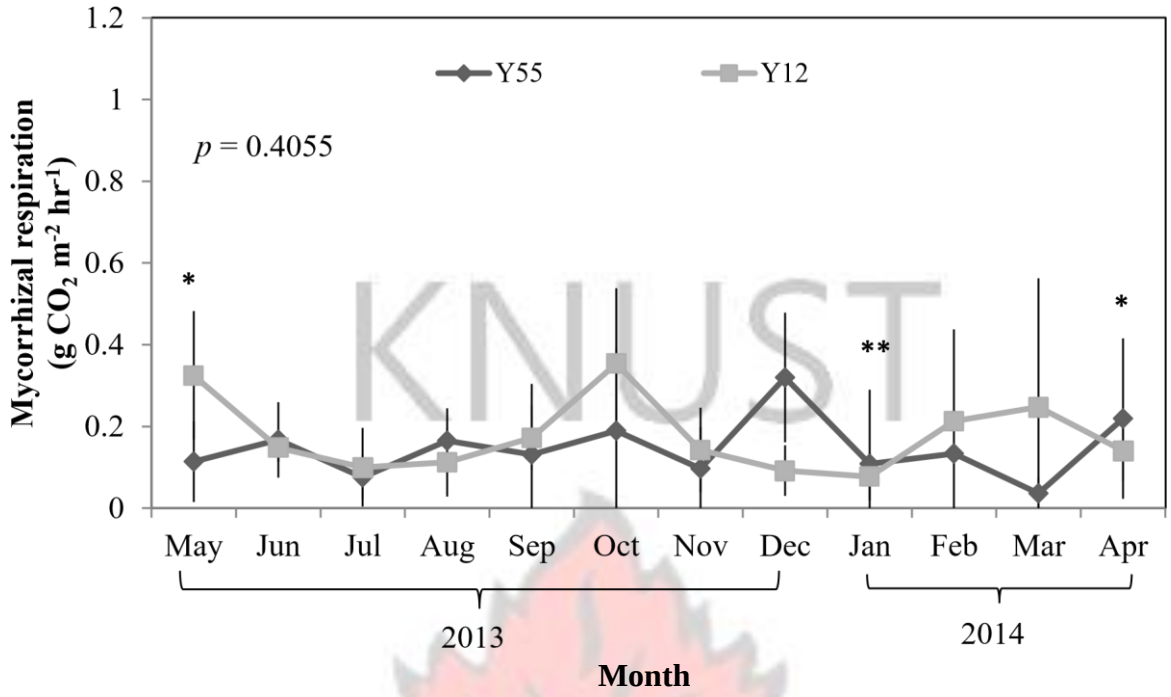


Figure 11: Monthly variation in mycorrhizal respiration for Y12 and Y55 measured over the study period. The *p* – value denotes significant level between sites tested for the entire study period using Student's *t*-test. Significant difference within the corresponding month is denoted by asterisk: * p < 0.05; ** p < 0.01 (Student's *t*test). Error bars represent standard deviation.

Average mycorrhizal respiration between the wet season and dry season was not significantly different ($p > 0.05$; Appendix 4D) at both sites. At Y12 site, average mycorrhizal respiration during the wet season (0.18 ± 0.07 g CO_2 m^{-2} hr^{-1}) was higher than dry season mycorrhizal respiration (0.17 ± 0.10 g CO_2 m^{-2} hr^{-1}) (Table 12).

Conversely, average mycorrhizal respiration at Y55 site was higher during the dry season (0.14 ± 0.11 g CO_2 m^{-2} hr^{-1}) than wet season (0.12 ± 0.07 g CO_2 m^{-2} hr^{-1}). Also the coefficient of variation (CV) in mycorrhizal respiration was higher in dry season than wet season at both sites (Table 12).

Table 12: Seasonal estimates of mycorrhizal respiration (g CO_2 m^{-2} hr^{-1}) for Y12 and Y55 site

Site	Season	Mean (±SD)	CV (%)
	Wet	0.18 (0.07)	40.89
Y12	Dry	0.17 (0.10)	60.26
	p - value	0.6445	
	Wet	0.12 (0.07)	62.75
Y55	Dry	0.14 (0.11)	78.24
	p - value	0.4501	

Values are results from monthly averages, SD is standard deviations, and CV is coefficient of variation. *P*-values denote significance level from repeated measures ANOVA.

4.4.4 Litter respiration

Monthly averages of litter respiration at both sites are shown in Appendix 4C. No significant difference in litter respiration for the entire study period was found between both sites (*t*-test, $p > 0.05$) although Student's *t*-test for each month showed litter respiration to be significantly higher at Y55 site during the month of September (Figure 12; Appendix 4C). Temporally, the seasonal pattern of litter respiration was more pronounced at Y12 than Y55 site (Figure 12).

Average litter respiration at Y12 site was significantly higher ($p = 0.0007$; Appendix 4D) during the wet season (0.38 ± 0.15 g CO_2 m^{-2} hr^{-1}) than dry season (0.18 ± 0.14 g CO_2 m^{-2} hr^{1}) (Table 13). At Y55 site, average wet and dry season litter respiration were not significantly different ($p > 0.05$; Appendix 4D) and constituted 0.24 ± 0.12 g CO_2 m^{-2} hr^{-1} and 0.22 ± 0.09 g CO_2 m^{-2} hr^{-1} for wet and dry season respectively. Additionally, dry season coefficient of variation (CV) (76.01 %) in litter respiration was higher than wet season (39.68 %) at Y12 site but lower (39.12 %) than wet season (51.14 %) at Y55 site (Table 13).

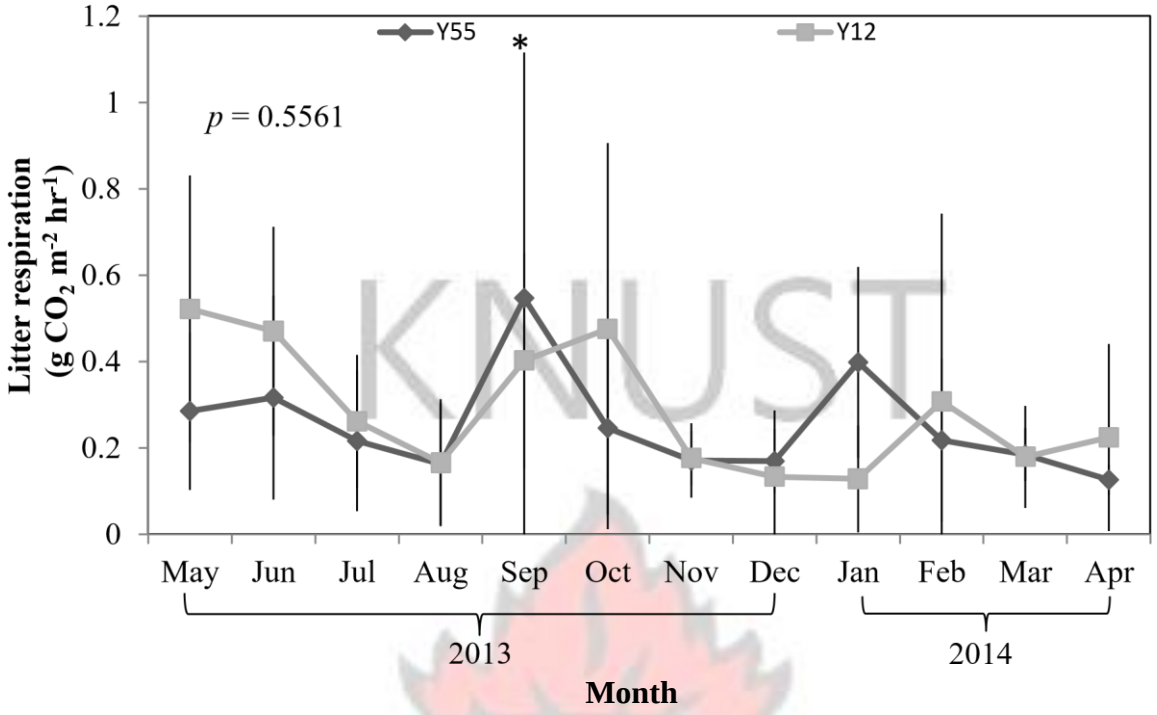


Figure 12: Monthly variation in litter respiration for Y12 and Y55 measured over the study period. The *p* – value denotes significant level between sites tested for the entire study period using Student's *t*-test. Significant difference within the corresponding month is denoted by asterisk: * $p < 0.05$ (Student's *t*-test). Error bars represent standard deviation.

Table 13: Seasonal estimates of litter respiration (g CO_2 m^{-2} hr^{-1}) for Y12 and Y55 site

Site	Season	Mean (±SD)	CV (%)
Y12	Wet	0.38 (0.15)	39.68
	Dry	0.18 (0.14)	76.01
	p - value	0.0007	
Y55	Wet	0.24 (0.12)	51.14
	Dry	0.22 (0.09)	39.12

p - value	0.6575

Values are results from monthly averages, SD is standard deviations, and CV is coefficient of variation. *P*-values denote significance level from repeated measures ANOVA.

4.4.5 Soil organic matter respiration

Monthly averages of soil organic matter respiration at both sites are shown in Appendix 4C. Soil organic matter respiration for the entire study period was significantly higher at Y12 than Y55 site. However, Student's *t*-test for each month showed no differences in soil organic matter respiration in individual months. Seasonally, the organic matter respiration at both sites exhibited a similar but not strong seasonal pattern (Figure 13).

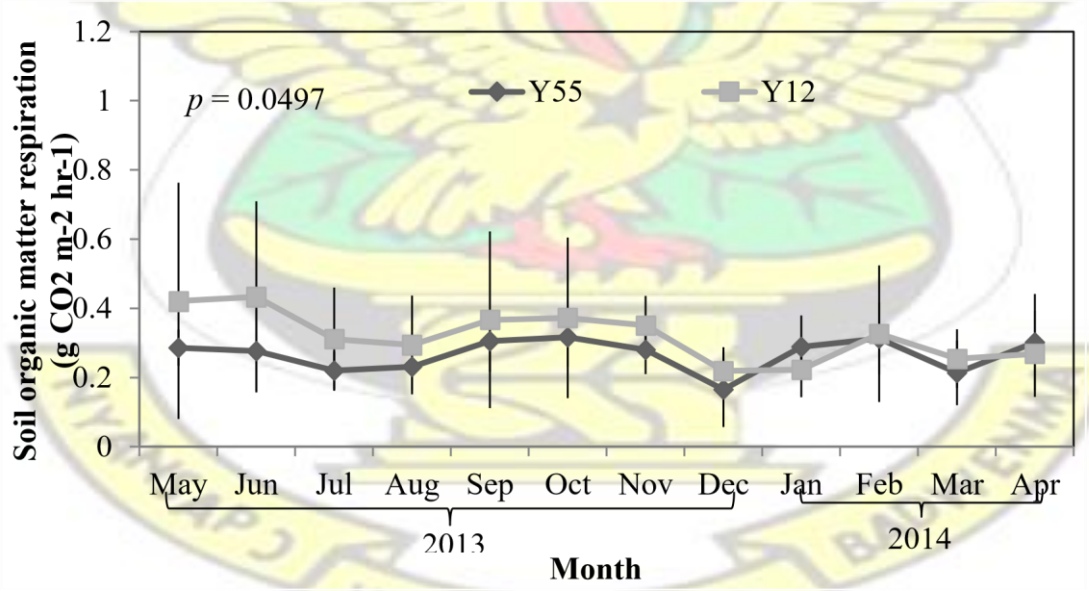


Figure 13: Monthly variation in soil organic matter respiration for Y12 and Y55 measured over the study period. The *p* – value denotes significant level between sites tested for the entire study period using Student's *t*-test. Error bars represent standard deviation.

At both sites, average soil organic matter respiration during the wet season and dry season was not significantly different ($p > 0.05$; Appendix 4D). Average soil organic matter respiration at Y12 site during the wet and dry season were 0.36 ± 0.18 g CO_2 m^{-2} hr^{-1} and 0.27 ± 0.06 g CO_2 m^{-2} hr^{-1} (Table 14). At Y55 site, average wet and dry season soil organic matter respiration were 0.27 ± 0.05 g CO_2 m^{-2} hr^{-1} and 0.26 ±0.06 g CO_2 m^{-2} hr^{-1} respectively. Furthermore, dry season coefficient of variation (CV) (22.36 %) in soil organic matter respiration was lower than wet season (49.25 %) at Y12 site but higher (22.32 %) than wet season (18.92 %) at Y55 site (Table 14).

Table 14: Seasonal estimates of soil organic matter respiration (g CO_2 m^{-2} hr^{-1}) for Y12 and Y55 site.

Site	Season	Mean (±SD)	CV (%)
Y12	Wet	0.36 (0.18)	49.25
	Dry	0.27 (0.06)	22.36
	p - value	0.0895	
Y55	Wet	0.27 (0.05)	18.92
	Dry	0.26 (0.06)	22.32
	p - value	0.3995	

Values are results from monthly averages, SD is standard deviations, and CV is coefficient of variation. *P*-values denote significance level from repeated measures ANOVA.

4.5 Annual magnitude of soil respiration and component contributions

Total annual soil respiration equated to 18.02 ± 0.71 SD Mg C ha^{-1} yr^{-1} and 17.83 ± 0.76 Mg C ha^{-1} yr^{-1} at 12-years post-logged site (Y12) and 55-years post-logged site (Y55) respectively (Table 15). Estimated annual soil respiration at Y12 and Y55 site was partitioned into 4.33 ±

0.14 and 6.17 ± 0.19 Mg C ha^{-1} yr^{-1} from root-and-rhizosphere, 3.06 ± 0.11 and 2.54 ± 0.09 Mg C ha^{-1} yr^{-1} from mycorrhizae, 4.94 ± 0.17 and 4.49 ± 0.15 Mg C ha^{-1} yr^{-1} from litter and 5.69 ± 0.09 and 4.63 ± 0.09 Mg C ha^{-1} yr^{-1} from soil organic matter respectively. This translates to an autotrophic respiration of 7.38 ± 0.24 and 8.71 ± 0.21 Mg C ha^{-1} yr^{-1} and a heterotrophic respiration of 10.63 ± 0.24 and 9.12 ± 0.20 Mg C ha^{-1} yr^{-1} for Y12 and Y55 respectively. A one-way analysis of variance (ANOVA) test carried out to determine within site differences among component respirations was significant at both sites ($p < 0.05$; Appendix 5). Tukey HSD post-hoc test revealed soil organic matter respiration to be significantly higher at both sites (Table 15).

Table 15: Annual soil respiration and component fluxes (Mg C ha^{-1} yr^{-1}) for Y12 and Y55 at Bobiri Forest Reserve.

	Autotrophs	*7.39*	*(0.24)*	*40.99*	
	Litter	4.94	(0.17)	27.42	
	Soil organic matter	5.69	(0.09)	31.59	
	Heterotrophs	*10.63*	*(0.24)*	*59.01*	
Site	Component	Mean	(±SD)	Percentage (%)	Difference
	Root-and-Rhizosphere	4.33	(0.14)	24.02	a
	Mycorrhizae	3.06	(0.11)	16.97	a
Y12	b				
					c
	Total soil	**18.02**	**(0.71)**	**100.00**	
	Root-and-Rhizosphere	6.17	(0.19)	34.58	a

	Mycorrhizae	2.54	(0.09)	14.26	a
	Autotrophs	*8.71*	*(0.21)*	*48.8 4*	
Y55 b	Litter	4.49	(0.15)	25.17	
	Soil organic matter	4.63	(0.09)	25.99	c
	Heterotrophs	*9.12*	*(0.20)*	*51.16*	
	Total soil	**17.83**	**(0.76)**	**100.00**	

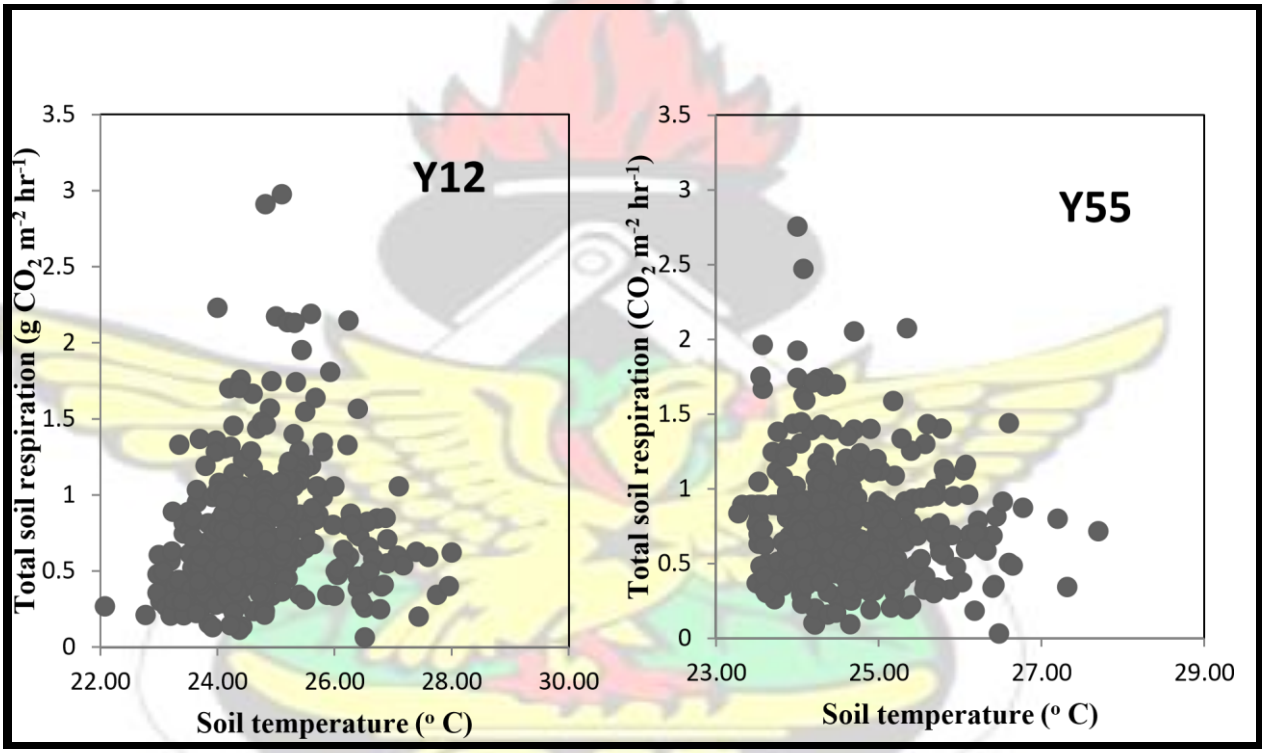
Autotrophs = respiration from root-and-rhizosphere and mycorrhizae; heterotrophs = respiration from litter and soil organic matter; letters in each site, represents relationship among component where values with the same letter in a column are not significantly different ($p < 0.05$) using Tukey HSD test.

In terms of percentages, estimated partitioned fluxes corresponded to percentages of 24.02 and 34.58 % for root-and-rhizosphere, 16.97 and 14.26 % for mycorrhizae, 27.42 and 25.17 % for litter and 31.59 and 25.99 % for soil organic matter at Y12 and Y55 respectively. This depicts a higher autotrophic percentage at Y55 (48.84 %) in comparison to Y12 site (40.99 %) and conversely, a higher heterotrophic percentage at Y12 (59.01 %) in comparison to Y55 site (51.16 %).

4.6 Factors influencing soil respiration

The daily soil respiration data from individual sample points were fitted against soil temperature and soil moisture using linear and several non-linear models however none was able to explain the collar to collar spatial variation in soil respiration due to considerable scatter (Figure 14). Nevertheless, better relationships for temporal variation were observed which took second order polynomial or quadratic functions. Between the two abiotic variables, soil moisture explained much variation at both plots although coefficient of determination (R^2) was relatively low at Y55 site (Figure 15). A quadratic-quadratic multiplicative function explaining the combined effect of soil temperature and soil moisture was able to improve the R^2's at both

plots, albeit marginally (Table 16). In all cases, soil respiration was more responsive to the abiotic factors at Y12 site than Y55 site, recording higher R^2s and significant relationships.



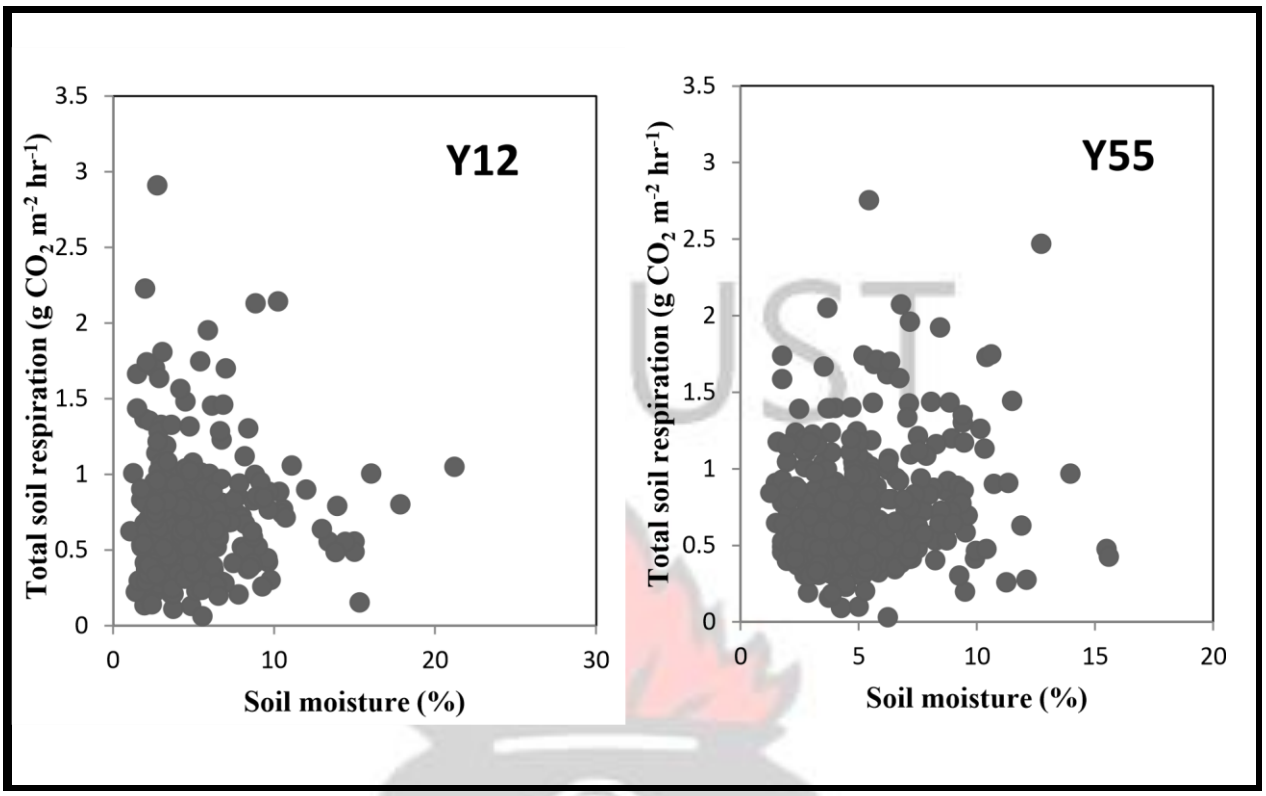
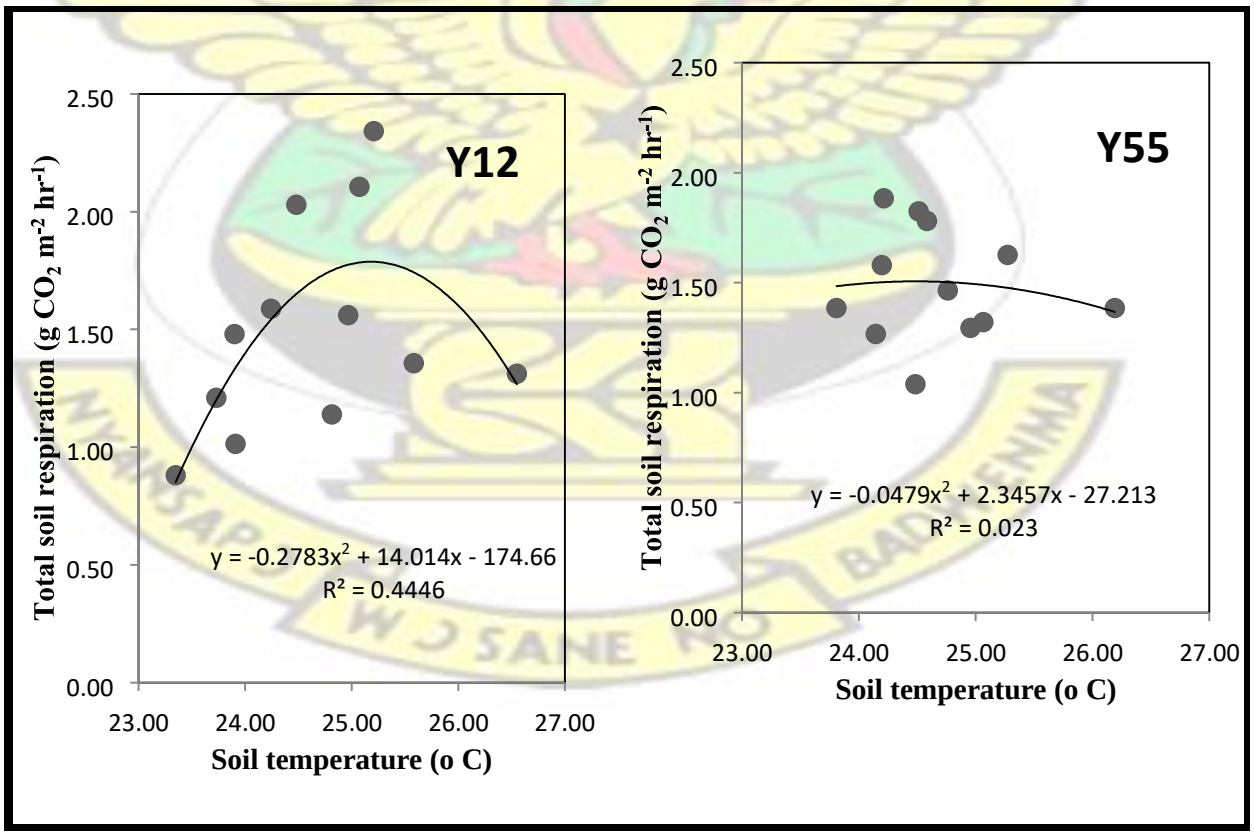


Figure 14: Daily total soil respiration as a function of soil temperature (upper panel) and soil moisture (lower panel) for Y12 and Y55 site.



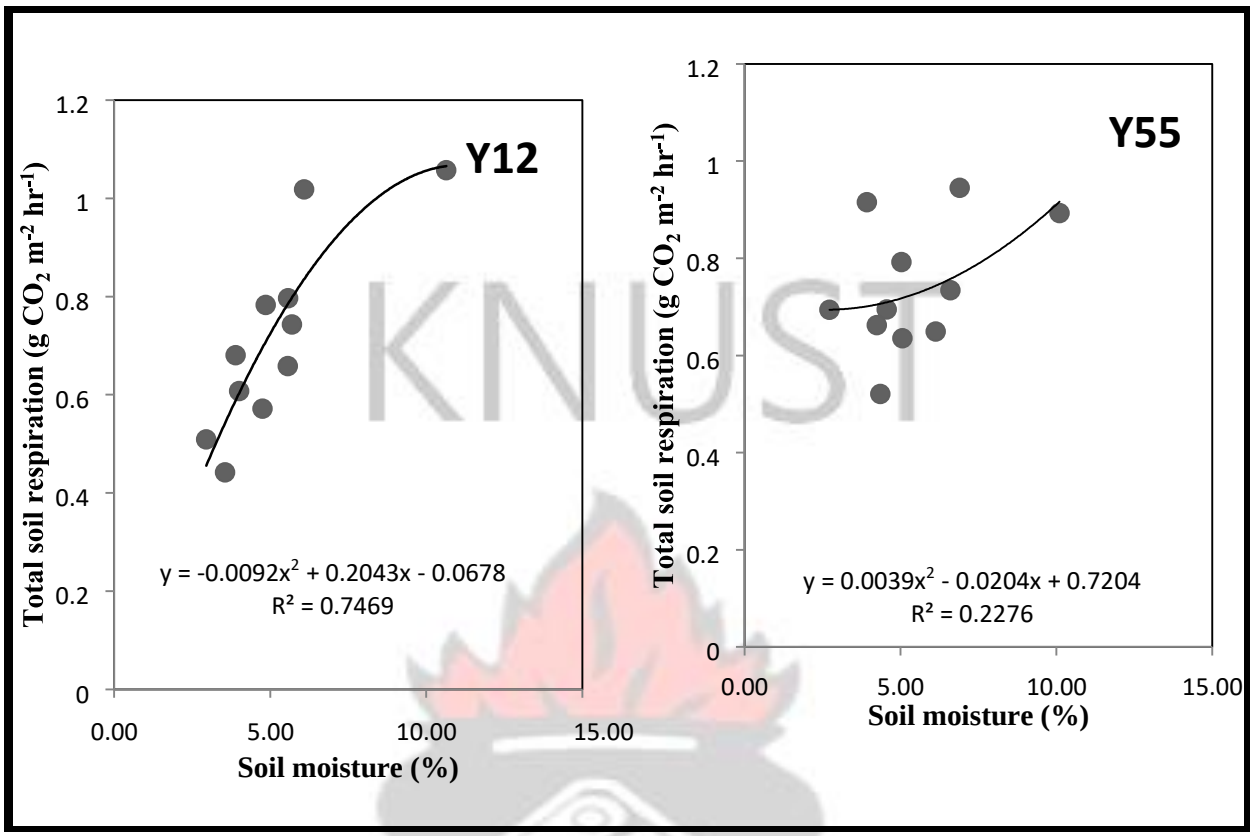


Figure 15: Averaged monthly soil respiration as a function of average soil temperature (upper panel) and average soil moisture (lower panel) for Y12 and Y55 site. Shown are the estimated model parameters and the coefficient of determination (R^2).

Table 16: Fitted relationships of soil respiration (g CO_2 ms^{-2} hr^{-1}) with soil temperature (T, ^oC) and soil moisture (θ, %) for Y12 and Y55 site.

$Soil respiration = aT^2 + bT + c$								
Site	*a*	*b*	*c*	*d*	*e*	*f*	R^2	*p*
Y12	-0.2783	14.014	-174.66	—	—	—	0.4446	0.071
Y55	-0.0479	2.3457	-27.213	—	—	—	0.023	0.106

$Soil respiration = a\theta^2 + b\theta + c$								
Site	*a*	*b*	*c*	*d*	*e*	*f*	R^2	*p*
Y12	-0.0092	0.2043	-0.0678	—	—	—	0.7469	0.004
Y55	0.0039	-0.0204	0.7204	—	—	—	0.2276	0.356

$Soil respiration = (aC^2 + b\theta + c)(dT^2 + eT + f)$								
Site	*a*	*b*	*c*	*d*	*e*	*f*	R^2	*p*

Y12	-0.002	0.035	-0.003	-0.515	25.712	-314.82	0.834	0.015
Y55	0.001	0.015	0.374	0.113	-5.766	74.748	0.287	0.837

The parameters *a, b, c, d, e, f* are model coefficients. R^2 and *p* represent coefficient of determination and *p*- value respectively.

CHAPTER FIVE

5.0 DISCUSSION

5.1 Seasonal variation in soil respiration

The seasonal variation in soil respiration has been studied in many ecosystems and depends on variation of environmental factors and ecosystem processes. Total soil respiration in both sites showed a significant seasonal change, whereby maximum mean total soil respiration rates were recorded during the wet seasons and lowest rates during the dry seasons. Similar decrease and increase in soil respiration with response to dry and wet seasons have been reported in previous studies (Davidson *et al.*, 2000; Valentini *et al.*, 2008). Dry season decrease in soil respiration principally occurs as a result of soil moisture deficit which limits microbial mobility and the breakdown of soil organic matter (Linn and Doran 1984; Davidson *et al.*, 2006a). In addition, moisture deficit leads to mortality of roots and the reduction of root growth and ion uptake by

existing roots (Burton *et al.,* 1998). This leads to low root respiration which was observed in the current study and previous studies (Burton *et al.,* 1998; Heinemeyer *et al.,* 2012). On the other hand, flushes of soil respiration following the re-wetting of soil beginning in the wet seasons has been caused by pulses of microbial activity or due to displacement of CO_2 in the soil by rain water (Birch, 1958; Davidson *et al.,* 2006a; Schwendenmann *et al.,* 2003). Preliminary results on litterfall (*unpublished data*) in both sites show trees to shed their leaves leading to a substantial amount of litterfall on the forest floor during the dry season and a lower amount during peak of the rainfall season. During the onset of the wet season when temperature and moisture are increasing, soil organisms are triggered to decompose forest floor litter accumulated during the dry season. This was evidenced by a higher wet season litter respiration which was more pronounced at Y12 site due to a greater ground surface litter stock and decomposition activity. In effect, there was an observed decline in total soil respiration, from a high value in May when the soil is wet to a low value in August when soil is dry and thereafter increased following re-wetting in September to October. Soil respiration rate decreased in November at both sites recording consistently low rates throughout the major dry season (December to March) when rainfall and soil moisture were at their low levels.

5.2 Magnitude of total soil respiration

In tropical forest ecosystems soil respiration is a very important component of the forest respiration budget (Metcalfe, 2008a). The annual total estimate of soil respiration of 18.02 and 17.83 Mg C ha^{-1} yr^{-1} for Y12 and Y55 sites respectively fall within the range of estimates from tropical forests ecosystems. In an earlier meta-analytical review of soil respiration studies, Subke *et al.* (2006) reported a range of 8.4 to 24.0 Mg C ha^{-1} yr^{-1} for tropical deciduous forests. Current studies from tropical Amazonian and Andean forests that employed similar methods and techniques as this study corroborate Subke's review and report a magnitude of

approximately 8 to 22 Mg C ha^{-1} yr^{-1} (Malhi *et al.*, 2014; da Costa *et al.*, 2014; Doughty *et al.*, 2014; Huasco *et al.*, 2014; Rocha *et al.*, 2014). Juxtaposing estimates with other ecosystems reveal relatively low estimates for temperate (9 Mg C ha^{-1} yr^{1}) and boreal (7 Mg C ha^{-1} yr^{-1}) forests (Subke *et al.*, 2006). This difference is influenced by confounding differences in climate (particularly rainfall), soil, vegetation characteristics and a relatively high decomposition and primary production in tropical forests in comparison to the other ecosystems (Luo and Zhou, 2006). For example, Fenn *et al.* (2010) in their study of soil CO_2 efflux in a temperate deciduous forest reported estimates of 4.1 Mg C ha^{-1} yr^{-1} where annual rainfall was relatively lower (725.88 mm) than rainfall from the sites of this study

(1709.6 mm).

5.3 Partitioning and component contributions

Various techniques to estimate soil respiration component contributions such as root exclusion, litter removal, girdling, etc. (Hanson *et al.*, 2000; Kuzyakov, 2006; Subke *et al.*, 2006; Luo and Zhou, 2006) have been applied by many studies. This study applied a root exclusion and litter removal technique using a combination of surface and deep collars also employed by a majority of recent partitioning studies in the Amazon and Andes region (Malhi *et al.*, 2014; da Costa *et al.*, 2014; Doughty *et al.*, 2014; Huasco *et al.*, 2014; Rocha *et al.*, 2014). As with all these soil respiration partitioning methods, the calculated fluxes are an approximation of existing field fluxes.

The use of ingrowth mesocosms with mesh windows, for mycorrhizae partitioning, which was first introduced by Johnson *et al*. (2001) in a grassland ecosystem and subsequently employed in a number of studies of forest ecosystems using several variants such as in a temperate coniferous forest (Heinemeyer *et al.*, 2007), temperate deciduous forest (Fenn *et al.*, 2010), broad-leaf and needle leaf forest (Moyano *et al.*, 2008), temperate deciduous oak forest (Heinemeyer *et al.*, 2012), boreal scots pine forest (Hasselquist *et al*., 2012) and moist tropical

forest (Nottingham *et al*., 2010) facilitates the estimation of mycorrhizal respiration by way of excluding roots but allowing extra-radical mycelium of the mycorrhizal fungus. Thus, the partitioning known as mycorrizal respiration is the respiration by only fungal hyphae grown by arbuscular and ecto- mycorrhizae across the soil matrix. Although it is well known that many mycorrhizal associations exist in connection with particular tree species
(Read, 1991; Cornelissen *et al.*, 2003), the design does not present these specific divisions. Root-rhizosphere respiration component contains the respiration of roots, rhizosphere organisms including all mycorrhizal networks in symbiosis with roots.

While roots were manually removed from the NLR (no litter and root) and NLRM (no litter, roots and mycorrhizae) collars to limit decomposition and to derive soil organic matter respiration, the absence of root exudates which are respired by soil microorganisms and responsible for priming effect could lead to underestimation of soil organic matter respiration and hence heterotrophic respiration. Priming effect is the enhanced microbial decomposition of older, more recalcitrant soil organic matter by the addition of fresh organic matter (Kuzyakov, 2000; Kuzyakov, 2002; Sayer *et al.*, 2007). In contrast, priming effect is included in the control collars hence could overestimate root-rhizosphere respiration. Priming effect is a process which is difficult to estimate in most exclusion methods.

In the absence of soil disturbance and beyond limitations in partitioning, the observed differences in magnitudes of respiration which was of the order, soil organic matter respiration > root-rhizosphere > litter> mycorrhizae and the seasonality of respiration of each component are evidence of an effective partitioning. Similarly, Fenn *et al.* (2010) observed a magnitude of the order soil organic matter > root-rhizosphere> mycorrhizae in their partitioning in a temperate deciduous forest. In explaining mycorrhizal activity within collars, Moyano *et al.* (2008) showed differing levels of inorganic nitrogen between partitioning treatments. The

observed decrease in nitrogen from soil cores within a 1 µm mesh bag to lowest levels within control cores indicated an uptake of nitrogen by mycorrhiza, with the implication that mycorrhizal hyphae had colonized the soil within the cores. Likewise in their pulse labeling experiment, Johnson *et al.* (2002) found that ^{13}C taken up by plants was respired from soil within a 35 µm mesh into which only mycorrhizal mycelia had access. Similarly, in a recent partitioning study on the effects of low and high nitrogen additions on soil CO_2 flux components, Hasselquist *et al*. (2012), observed CO_2 fluxes from ectomycorrhizal hyphae to be nearly twice as high in low N treatment compared to the control plot. In contrast, ecto-mycorrhizal hyphae respiration was significantly reduced in high N treatment which indicated that mycorrhizal hyphae colonization was negatively affected by high nitrogen addition. In absolute terms, analysis of soils within collars for mycorrhizal presence and absence would increase the robustness of further studies employing this method.

In effect, the estimate of 40.99 % (Y12) and 48.84 % (Y55) for autotrophic respiration and 59.01 % (Y12) and 51.16 % (Y55) for heterotrophic respiration obtained from this study compares well with the estimates from similar Amazonian studies which report a range of approximately 14 to 63 % for autotrophic contribution to total respiration and a heterotrophic contribution of a range of 40 to 78 % (Malhi *et al.,* 2014; da Costa *et al.,* 2014; Doughty *et al.,* 2014; Huasco *et al.,* 2014; Rocha *et al.,* 2014). Additionally, the estimates of rootrhizosphere contribution (24.02 % for Y12 and 34.58 % for Y55) falls within the overall global reported contribution of 10 to 90 % (Hanson *et al*. 2000) while the heterotrophic estimate (59.01 % for Y12 and 51.16 % forY55) falls within global mean annual heterotrophic contribution (i.e. the sum of litter and soil organic matter respiration) from tropical deciduous forests with a reported range of 27 to 76 % (Subke *et al.,* 2006).

5.4 Age-related effects on soil respiration and component contributions

In the current study, soil respiration was looked at by comparing two sites subject to the same method of selective logging which occurred at different times, hence producing different post-logging ages. Total soil respiration for the younger site (12 years post-logged, Y12) was higher than the older site (55 years post-logged, Y55), although differences were not significant. An age-related study by Jassal *et al.*, 2012 observed soil respiration in a 21-yearold Douglas-fir stand to be appreciably higher than in a 60-year-old stand at Vancouver Island in Canada. Even as gross ecosystem productivity was lower, this was attributed to abundant deciduous understory and a relatively thicker Litter-fermenting-humified layer at the younger stand.

Similarly, Saiz *et al.* (2006) found total soil respiration to similarly decrease with age over a Sitka spruce chronosequence (10, 15, 31 and 47 year old) plantation in Central Ireland although in their case, the relative contribution of both autotrophic and heterotrophic respiration decreased with stand age which was explained by a decrease in fine root biomass and activity with aging.

In the present study, the older site (Y55) recorded a higher root-rhizosphere and hence autotrophic respiration than the younger site (Y12). Besides, increase in autotrophic contribution with stand age was in agreement with increased root biomass. Similarly, the contribution of autotrophic respiration was found to increase with stand age in *Pinus elliottii* plantations, from 51% in a 9-year-old stand to 62% in a 29-year-old stand due primarily to the nearly threefold increase in live root biomass (Ewel *et al.*, 1987). Furthermore, soil at Y55 site was more fertile which conflicts with allocation theory that posits plants growing in resource-rich environments to invest all newly acquired photosynthate to leaves rather than roots since allocation to non-photosynthetic tissue gives no return in future carbon acquisition (Bloom *et al.*, 1985; Friedlingstein *et al.*, 1999). The surprise was in pact with Doughty *et al.* (2013) who

also recorded higher fine root productivity and root-rhizosphere respiration in a nutrient rich *terra preta* soil compared to an unfertile site of a lowland tropical Amazonia forest. The foregoing may suggest a maturing forest investing in more roots for structural support and nutrient allocation.

Contrariwise, heterotrophic respiration from the microbial breakdown of belowground litter and soil organic matter decomposition was higher at Y12 than at Y55 site with a significant soil organic matter respiration at Y12 site, which obviously contributed to the higher absolute value of total soil respiration. This suggests that even though root-rhizosphere respiration at Y12 is lower, turnover of litter at Y12 may be higher than at the more nutrient-rich Y55 site (see also Sulzman *et al.,* 2005).

5.5 Factors influencing total soil respiration

Although soil temperature is recognized as the most influential factor of soil respiration and has been able to explain the temporal variation in many ecosystems (Lloyd and Taylor, 1994; Fenn *et al.,* 2010) it has not been able to do so in others, particularly in tropical regions where soil temperatures are high and relatively invariable (e.g. Davidson *et al.,* 2000; Schwendenmann *et al.,* 2003; Metcalfe *et al.,* 2007; Valentini *et al.,* 2008). Furthermore, in most tropical forests an intersecting effect between soil temperature and soil water has been observed where it may be very difficult to distinguish between the effect of temperature and soil water content as both rise and fall together during the same season (Kiese and Butterbach-Bahl, 2002; Epron *et al.,* 2004; Valentini *et al.,* 2008; Zimmermann *et al.,* 2010). A similar response occurred in both sites whereby temperature and soil moisture were observed to be at a high in May and decline together up to August. Similar decline was observed after the minor wet season till December. Hence, the influence of soil temperature on temporal variation in

soil respiration may have been disguised by the effect of soil moisture leading to weaker relationships between soil respiration and soil temperature.

The ability of soil respiration to respond to soil moisture is consistent with most tropical forest ecosystems studies (e.g. Davidson *et al.*, 2000; Schwendenmann *et al.*, 2003; Epron *et al.*, 2004; Metcalfe *et al.*, 2007; Valentini *et al.*, 2008). Similarly, parabolic empirical functions describing the temporal variation in soil respiration and moisture observed in this study were likewise observed by Schwendenmann *et al.* (2003) and Valentini *et al.* (2008) in tropical forest ecosystems. Davidson *et al.* (1998) reported that aside soil temperature and soil water content influencing soil respiration independently, these factors confound to influence soil respiration and this has been demonstrated by many research works (e.g. Valentini *et al.*, 2008; Zimmermann *et al.*, 2009; Chen *et al.*, 2010c; Lai *et al.*, 2012; Campos, 2014). In the current study, soil respiration was better explained by the combined effects of soil temperature and soil water content. In addition, the empirical models were stronger at Y12 than Y55 site. This could be due to the higher spatial variation in soil respiration, the differences in optimum water levels or differences in soil physical characteristics which influence porosity and CO_2 diffusivity differently (Bouma and Bryla, 2000). Similarly, Schwendenmann *et al.* (2003) observed differences in curves and optimum water levels for six sites with different soil characteristics in an old-growth tropical forest in Costa Rica. Similarly Jassal *et al.* (2012) observed soil respiration in a 21-year-old Douglasfir stand to be more responsive to changes in soil temperature and moisture than in a 60-yearold stand in Canada. They attributed this to abundant deciduous understory and a relatively thicker Litter-fermenting-humified layer which influenced soil water stress at the younger stand.

Furthermore, the empirical functions relating the collar-to-collar spatial variation in soil respiration and soil moisture in this study were generally weak as has been similarly observed

in other studies (Davidson *et al.,* 2000; Schwendenmann *et al.,* 2003; Metcalfe *et al.,* 2007; Valentini *et al.,* 2008). Metcalfe *et al.* (2007) in their study of soil respiration in four sites of a tropical Amazonian forest observed considerable within-site spatial heterogeneity in soil respiration whereby soil temperature and moisture could not explain the observed variation in soil respiration. Within site spatial variation was only explained when a two month regression of soil respiration with root and litter mass and their specific respiration rates were able to explain about 44% of observed variation. Similarly, Davidson *et al.* (2000) in their study of soil water content effect on soil respiration in forests and cattle pastures of eastern Amazonia, observed a correlation between soil respiration and the logarithm of matric potential and the cube of volumetric water content. However they observed considerable scatter and concluded that relating rates of soil respiration to water and temperature measurements made at some arbitrarily chosen depth of the surface horizons is simplistic. They therefore recommended the measurements of temperature, water content and CO_2 production for each soil horizon to help in defining temperature and moisture functions. Ohashi *et al.* (2008) found that local spatial differences in temperature could explain spatial variation in soil after controlling data for "CO_2 hotspots". They suggested the unevenness of canopy structure and underground vegetation to generate heterogeneity in the sun's radiation reaching the forest floor, leading to patchiness in temperature in the litter and soil surface layers. Their conclusion was that spatial differences in soil CO_2 efflux might have been controlled by multiple factors whose effects vary with time. While soil water content is a better soil abiotic factor controlling seasonal variation of soil respiration in this ecosystem, it does not account for spatial variability over the experimental sites. On the other hand, within site spatial variation of soil respiration has often been related to variation in biotic factors such as changes in root biomass, litter amount, soil organic matter, microbial biomass, soil chemistry or soil physical properties. It is argued that spatial variation in soil respiration is controlled by biotic factors in this ecosystem and needs further exploration.

5.6 Implications of the study

5.6.1 Implications for forest management

There is increasing need to understand the influence of management practices on forest carbon balance. While this is critical, abundant evidence from various studies in Ghana indicate that selective logging, whether employed for commercial purpose or silvicultural intervention introduces a level of disturbance that can influence carbon dynamics (e.g. Adu- Bredu *et al.*, 2008; Asante, 2010; Djagbletey, 2014). The immediate belowground effects of logging as aforementioned can have long term recovery effects (Jusoff and Majid, 1992; Pinard *et al.*, 1996) which cannot be discounted.

From the results, it is difficult to determine if the dynamics reported are the results of longterm logging effects. Therefore, it cannot be said categorically whether the results imply a successful recovery of belowground function at Y55 (the site exceeding the 40-year felling cycle). As exploratory investigations in congruence with assessment of various recovery indicators, particularly in relation to the main disturbance types (i.e. skid trails and loading bays) were not duly accomplished, the casual comparison between both plots remains an inadequate supposition. This is so even as recent long-term studies (e.g. Hawthorne *et al.*, 2012) employing a broad range of recovery indicators as basal area, mortality rate, diameter increment and changes in the balance of tree guilds (Pioneer Index) indicates Ghana's commercial logging practices to be short of sustainability on the current 40-year felling cycle. With this in motion, and until more research is conducted and greater robustness in observations and results achieved, appropriate caution needs to be applied in trying to extrapolate conclusions. However, while the demand to pursue the full components of Reduced Impact Logging techniques (RIL) (Pinard and Putz 1996; Medjibe, 2011) to curb deleterious effects of logging on forest carbon balance and biodiversity still remains on board, good forest

management should employ the full scope of sustainable practices such as proposed by the International Tropical Timber Organization (ITTO).

Compared to the 55 years post logged site, the study confirms that litter and soil organic matter respiration (heterotrophic respiration) is a significant component of total soil respiration at the 12 years post logged site, which signifies the accumulation of forest floor harvest residue at the site. During rainfall periods following extreme drought, the consequence of large residue could be an increased microbial activity which would enhance soil respiration and thus disrupt the carbon budget— hence accelerate climate change. It would therefore be proper for forest managers to monitor litter stocks and residue, particularly during and after times of harvesting. A first step in the right direction will be to reduce logging practices that produce a lot of forest floor residue. Similarly, a strong seasonal change in soil respiration, whereby significantly higher average fluxes occurred during the wet season and lower fluxes occurred during the dry season should prompt managers to stick to logging in the dry season as already prescribed by the logging manual. This should avoid enhanced emissions of CO_2. In all, soil respiration should be given more attention in forest management forecasts and practices.

5.6.2 Implications for climate change

It has long been established that the current climate change is due to consistent anthropogenic perturbations to atmospheric greenhouse gas concentrations. Elevated atmospheric CO_2 concentration results in global warming which could on the other hand substantially stimulate respiration, resulting in more release of CO_2 to the atmosphere (Cox *et al.,* 2000). To address climate change, the United Nations Framework Convention on Climate Change (UNFCCC) through its 15th session of the Conference of Parties (COP 15) at Copenhagen in 2009, brought to the fore, the Reduced Emissions from Deforestation and Forest Degradation Plus (REDD+)

mechanism. The core framework of REDD+ is for developed countries to finance developing countries including Ghana to pursue low-emission activities while developing countries will trade carbon credits (equal to the carbon sequestered by their preserved forests) on the carbon market to developed countries that require carbon offsets. Hence, REDD+ includes the implementation of the following mitigation activities: (a) Reducing emissions from deforestation; (b) Reducing emissions from forest degradation; (c) Conservation of forest carbon stocks; (d) Sustainable management of forest; and (e) Enhancement of forest carbon stocks in developing countries.

In implementing fully the REDD+ mechanism and other similar strategies, tropical countries are also required to periodically report on their national inventories of sector anthropogenic GHG emissions and sinks, including the Land Use, Land-Use Change and Forestry (LULUCF) sector (UNFCC, 1992). Similarly, countries are to put in place robust and transparent national Monitoring, Reporting and Verification (MRV) systems (Petrokofsky *et al.,* 2012), of which details of the developments of such approaches are undergoing international discussions (Vargas *et al.,* 2013). Elements of MRV methodologies include forest inventories, remote sensing, intensively monitoring sites and models (Birdsey *et al.*, 2013). To reduce uncertainty and help explain observed changes that result from management or disturbance, Birdsey *et al.* (2013) and Vargas *et al.* (2013) advocate the use of intensive monitoring sites that involve estimates of processes of CO_2 uptake (gross primary production), sequestration, release to the atmosphere (ecosystem respiration) and lateral transport of carbon through erosion, anthropogenic transport or harvest – a complete net ecosystem carbon budget (NECB) approach. This will give information on carbon stocks and rates of change that may not easily be quantified over large areas by extensive field measurements (Birdsey *et al.,* 2013). Additionally, when fused into a multi-method approach involving the use of remote sensing and national forest inventories, estimates from intensive monitoring sites can be used to

develop emission factors or models to scale-up estimates to regional and national levels as well as design forest management systems for increasing carbon stocks (Birdsey *et al.,* 2013).

Currently, Ghana which is a signatory to the UNFCCC, has initiated its REDD+ readiness process, and completed a design phase of its forest reference emission levels as well as a national MRV system which is geared towards full implementation of the REDD+ mechanism. Soil respiration estimates from the current study should aid in the development of net ecosystem carbon budgets and augment multi-method approaches that seek to establish standard operating procedures for forest emissions levels for REDD+ projects and other related climate change mitigations strategies.

5.7 Limitation of the study

Each 1.0 ha sample plot was established around remaining stumps of harvested trees and based on analysis within these single-plots, it has been surmised that the temporal dynamics and relative magnitude of soil respiration and its component fluxes, in addition to ancillary measurements are representative of the entire forest compartment and that there exist no larger-scale spatial variations. However, each compartment is plagued with its own level of visible logging disturbance or ‘‘scars’’ including old roads and loading bays, skid trails, and gaps (Hawthorne *et al.,* 2012) which may vary in intensity along each compartment. In addition soil respiration is a complex and heterogeneous process, which has been shown to vary considerably in space with differences in measured fluxes from individual microsites to several meters apart even within an area of similar soil drainage class and vegetation type (Davidson *et al.,* 2002b). Hence, the results may not be representative of estimates across the entire 128 ha compartment. Therefore, caution is required when interpreting these results particularly with regards to the entire compartment. Measuring soil respiration within multiple sites across each compartment would have been superlative but constrained due to practical and financial

limitations. The need for additional replicate plots would help build the strength of results and observed relations.

CHAPTER SIX

6.0 CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

This study examined the variation and magnitude of respiration from soil and its components as well as determined the influence of soil temperature and soil moisture on soil respiration in two sites of contrasting post-logged ages— 12 and 55 years post-logged. At both sites, there existed a strong seasonal change in total soil respiration whereby significantly higher average fluxes occurred during the wet season and lower fluxes during the dry season. Similarly, respiration of component part changed between the wet and dry season nevertheless, significant changes were observed for root-and-rhizosphere respiration at both sites.

The estimated annual magnitude of total soil respiration was higher at the 12 years post logged site although plot differences were not significant. Partitioning revealed a higher heterotrophic respiration (litter and soil organic matter respiration) which obviously contributed to the higher absolute value of total soil respiration. Contrariwise, 55 years postlogged site recorded a higher root-and-rhizosphere respiration, consequently, a higher autotrophic respiration amid a nutrient-rich soil environment. This insight portends a forest maturing and possibly recovering from disturbance, although additional research needs to corroborate the conclusion.

In comparison to soil temperature, soil moisture was the better predictor, able to explain reasonable variation in total soil respiration. However, soil temperature as a second predictor was able to improve the model predictive power although marginally. None of the abiotic factors explained satisfactorily the collar-to-collar spatial variation in soil respiration hence it was suggested that there existed potential underlying biotic factors influencing soil respiration.

The study presents the first results of soil respiration in a moist-semi deciduous forest in Ghana and demonstrates the importance of separating total soil respiration into source components when studying the influence of forest age.

6.2 Recommendations

More ecophysiological studies in these study sites will be required to fully comprehend the intricate nature of soil respiration. One area is the study of the vertical variation of soil respiration at deeper soil depths where soil microbes and deep roots respond differently to soil temperature and moisture contents (Davidson and Trumbore, 1995; Risk *et al.,* 2002; Fierer *et al.,* 2003). Also, experiments should investigate the aboveground photosynthetic activity and allocation patterns of photosynthates to the rhizosphere which drives soil respiration. In that regard, studies that employ girdling and isotopic labeling will be essential. Future studies should also explore in detail the response of microsites such as skid trails and loading bays on soil respiration. Lastly, the significance of this study ought to be replicated not only in other sites and forest ecosystems in Ghana but expanded to capture the wide range of ecological situations. This need is warranted since this will enable national and regionalscale analyses for formulation of CO_2 budgets beneficial for carbon monitoring, reporting and verification.

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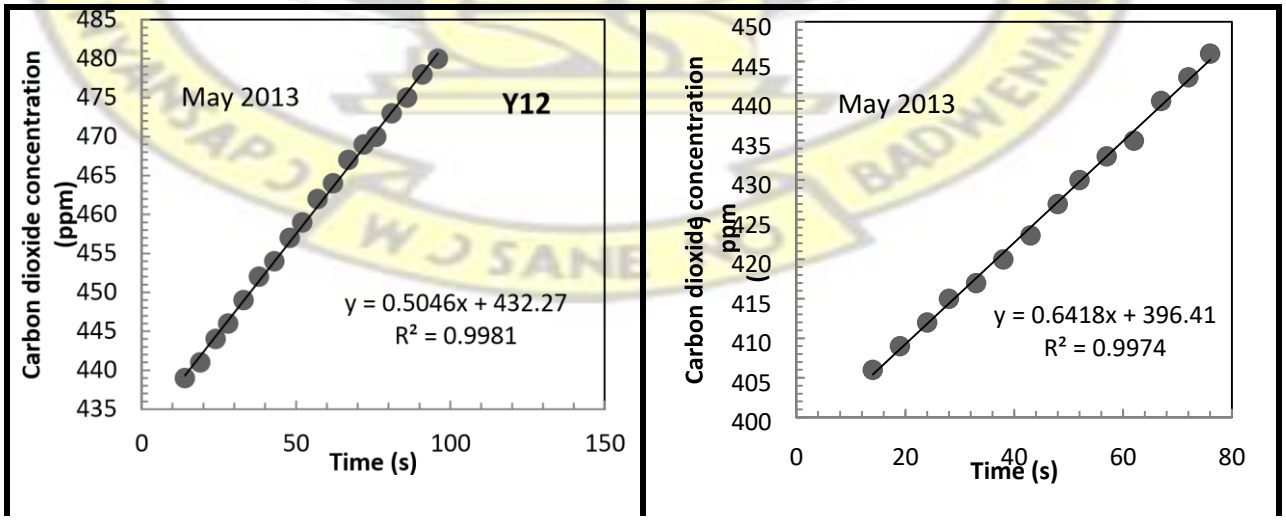
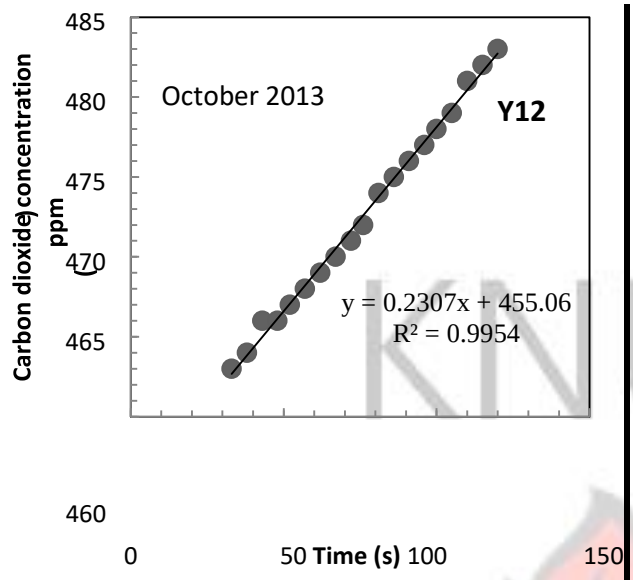
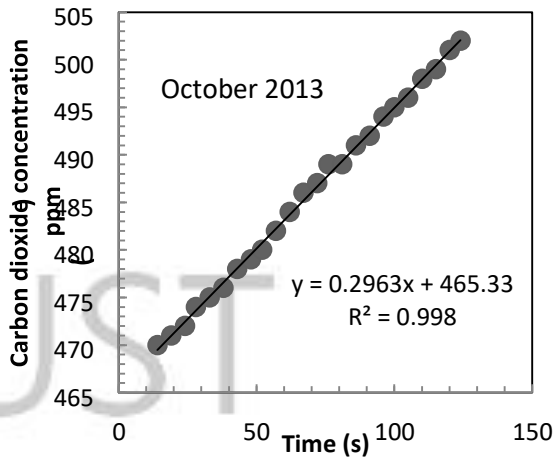
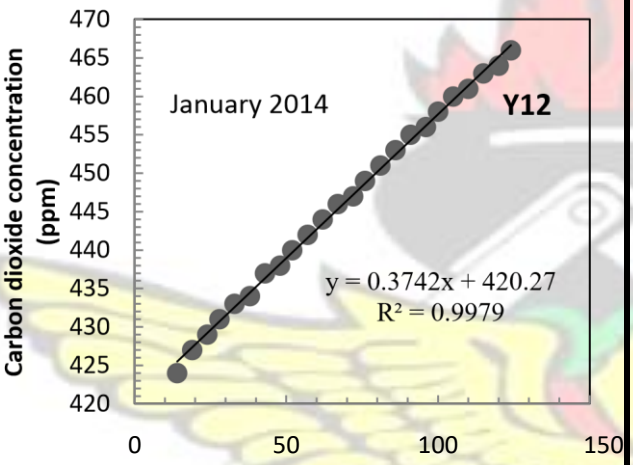
APPENDICES

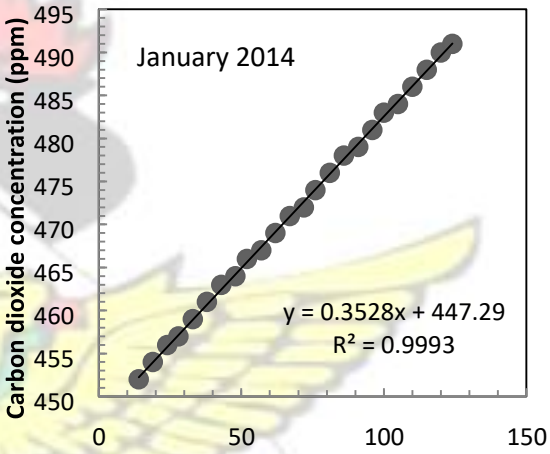
APPENDIX 1A: Changes in the carbon dioxide (CO_2) concentration (ppm) in the soil respiration chamber with time (seconds) in some subplots for selected months at Y12 (left panel) and Y55site (right panel).











Appendix 1B: Rate of change of CO_2 (ppm s^{-1}) for Y12 and Y55 site.

Month	Y12 Mean	Y12 Max	Y12 Min	Y12 SD	Y55 Mean	Y55 Max	Y55 Min	Y55 SD
		2.87	0.21			1.28	0.17	
May	1.11			0.6	0.65			0.27
Jun	0.74	1.54	0.12	0.37	0.79	1.5	0.3	0.29
Jul	0.57	1.2	0.1	0.23	0.7	1.36	0.32	0.28
Aug	0.7	2	0.35	0.32	0.58	1.39	0.24	0.31
Sep	0.97	2.11	0.37	0.43	0.83	1.81	0.08	0.45
Oct	0.98	2	0.55	0.39	0.77	1.27	0.26	0.31
Nov	0.75	3.48	0.25	0.59	0.59	1.24	0.27	0.25
Dec	0.41	1.31	0.13	0.24	0.54	2.03	0.13	0.35
Jan	0.47	1.26	0.14	0.24	0.44	1.51	0.08	0.25

Feb	0.52	1.39	0.19	0.23	0.63	1.36	0.18	0.25
Mar	0.59	1.66	0.07	0.3	0.59	1.54	0.03	0.31
Apr	0.62	1.38	0.28	0.24	0.57	2.3	0.23	0.38
Mean	0.7	—	—	0.22	0.64	—	—	0.11

Max, Min and SD represent maximum rate, minimum rate and standard deviation respectively.

Appendix 1C: Monthly atmospheric pressure (Pa) for Y12 and Y55 site measured for the study period.

	Y12				Y55			
Month	Mean	Max	Min	SD	Mean	Max	Min	SD
May	986.10	987	985	0.86	983.00	985	982	0.97
					986.32	987	985	0.91
Jun	988.84	990	987	1.05	987.38	990	986	0.99
					986.97	990	986	1.07
Jul	990.61	994	987	2.09	988.18	990	984	1.34
					985.33	988	982	2.09
Aug	989.59	993	988	1.28	983.59	985	979	1.88
					985.06	986	981	1.61
Sep	989.70	993	987	2.44	982.41	985	981	1.69
					984.12	987	982	1.14
Oct	987.00	989	985	1.13	981.06	984	980	1.79
					984.62	990	983	2.37
Nov	987.18	990	982	2.8				
Dec					984.84	—	—	2.14
989.45	990	989	0.51					
Jan	984.23	987	983	1.38				
Feb	985.45	987	983	1.26				
Mar	986.81	989	985	1.26				
Apr	988.64	992	985	2.03				
Mean	987.8	—	—	1.96				

Max, Min and SD represent maximum rate, minimum rate and standard deviation respectively.

Appendix 2: Monthly rainfall and air temperature for the study site measured over the study period.

Month	Rainfall (mm)		Maximum Air temperature (^{o}C)		Minimum Air temperature (^{o}C)	
	Mean	(±SD)	Mean	(±SD)	Mean	(±SD)
May	397	(±26.14)	31.57	(±1.18)	23.19	(±1.31)
Jun	133.4	(±11.7)	29.03	(±1.64)	22.94	(±0.61)
Jul	120	(±11.47)	26.15 ~	(±1.64)	21.82	(±0.86)
Aug	12.6	(±1.61)	26.21	(±1.29)	21.68	(±0.84)
Sep	457.1 #	(±35.11)	28.72	(±1.42)	22.14	(±0.5)
Oct	181.5	(±11.77)	29.33	(±2.01)	22.3	(±0.67)
Nov	114.8	(±8.25)	30.63	(±0.86)	22.71	(±0.88)
Dec	10 ~	(±2.75)	30.44	(±1.34)	20.36 ~	(±2.16)
Jan	65.8	(±23.77)	31.87	(±1.34)	22.87	(±1.74)
Feb	22.7	(±4.43)	32.24	(±1.22)	22.14	(±1.63)
Mar	65.4	(±13.38)	32.58 #	(±1.55)	22.76	(±1.67)
Apr	129.3	(±8.25)	31.76	(±1.78)	23.67 #	(±2.11)
Total	1242.5	(±13.22)	Average 30.18	(±1.44)	22.46	(±1.25)

Data were obtained from FORIG weather station (6˚44'N, 1˚30'W) located at 21 km from the site sites. # Highest rainfall/temperature values; ~lowest rainfall/temperature values.

Appendix 3A: Day-time average soil temperature (° C) for Y12 and Y55 site measured over the study period.

Site	Statistic	Month												Mean
		May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	
Y12	Mean	25.21	24.24	23.9	23.73	24.48	25.07	24.97	23.35	23.91	24.81	26.55	25.58	24.65
	Max	25.80	24.93	24.44	25.20	26.24	27.14	26.52	24.18	25.88	24.86	28.00	27.95	—
	Min	24.20	23.84	23.28	19.5	24.00	24.10	24.38	22.08	19.58	24.79	25.63	24.32	—
	SD	0.42	0.25	0.31	1.12	0.38	0.65	0.41	0.41	1.37	0.02	0.56	0.86	0.90
	CV	1.68	1.03	1.28	4.72	1.56	2.57	1.65	1.76	5.74	0.07	2.10	3.37	2.29
Y55	Mean	25.27	24.51	24.2	23.81	24.21	24.58	24.95	24.14	24.48	24.76	26.19	25.06	24.68
	Max	26.40	25.18	25.30	24.40	24.63	24.62	25.30	24.63	25.20	25.75	27.70	26.10	—
	Min	23.76	24.00	23.50	23.50	23.90	23.33	24.45	23.60	20.70	23.28	25.08	23.76	—
	SD	0.56	0.25	0.33	0.25	0.19	0.40	0.22	0.25	0.95	0.55	0.55	0.47	0.64
	CV (%)	2.20	1.00	1.36	1.04	0.80	1.48	0.87	1.03	3.90	2.21	2.09	1.89	1.66
	p - value	0.576	**0.000**	**0.000**	0.686	**0.001**	**0.000**	0.883	**0.000**	**0.049**	0.585	**0.009**	**0.003**	0.939

Values are results from daily plot averages, Max is maximum, Min is minimum, SD is standard deviation, and CV is coefficient of variation, *p*-value 0.000 indicates $p < 0.0001$.

Appendix 3B: Day-time average soil moisture (%) for Y12 and Y55 site measured over the study period.

Site	Statistic	Month												
		Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Mean	
Y12	Average	5.58	5.7	4.01	6.09	10.64	4.86	3.56	2.95	4.76	5.57	3.9	5.24	
	Min	1.5	2.25	1.75	1.5	5.9	1.26	1.95	1.43	1.07	2.05	1.78	—	
	Max	15.32	15	9.64	13.92	21.2	9.28	7.8	5.18	14.42	17.84	12.98	—	
	SD	3.18	3.08	1.95	3.14	3.38	2.2	1.22	0.96	2.82	2.87	2.1	2.05	
	CV	56.94	54.06	48.61	51.57	31.74	45.32	34.12	32.46	59.36	51.64	53.72	47.23	
Y55	Average	3.92	5.03	2.72	6.9	10.1	6.13	5.07	4.35	6.6	4.56		5.42	
	Min	1.48	1.8	1.25	2.92	7.06	2.18	2.48	2.13	2.44	1.96	4.24	2.3	—
	Max	9.32	11.25	5.5	15.48	16.92	9.45	9.4	6.57	13.96	8.06	6.78	—	
	SD	2	2.46	1.12	2.89	2.13	1.62	1.72	1.13	2.16	1.34	1.1	1.98	
	CV (%)	51.05	48.92	41.07	41.94	21.11	26.36	33.86	25.98	32.77	29.32	25.86	34.39	
	p - value	**0.0122**	0.3262	**0.0013**	0.2753	0.4411	**0.0085**	**0.0001**	**0**	**0.0035**	0.0687	0.4076	0.8346	

Values are results from daily plot averages, Max is maximum, Min is minimum, SD is standard deviation, and CV is coefficient of variation, *p*-value 0.0000 indicates $p < 0.0001$ tested with Student's *t*-test.

Appendix 3C: Day-time soil temperature (° C) for soil respiration partitioning collars at Y12 and Y55 site measured over the study period.

Control NL NLR NLRM

Site	Month									*p* - value
		Mean (± SD)		Mean (± SD)		Mean (± SD)		Mean (± SD)		
	May	25.16 (± 0.36)	a	25.19 (± 0.38)	a	24.57 (± 0.82)	a	25.16 (± 0.46)	a	0.056
	June	24.10 (± 0.23)	a	24.10 (± 0.27)	a	24.09 (± 0.24)	a	24.07 (± 0.2)	a	0.989
	Jul	24.08 (± 0.41)	a	24.03 (± 0.37)	a	24.02 (± 0.37)	a	24.02 (± 0.43)	a	0.989
	Aug	23.97 (± 0.48)	a	23.92 (± 0.42)	a	23.94 (± 0.44)	a	23.91 (± 0.50)	a	0.994
	Sep	24.97 (± 0.98)	a	24.93 (± 0.97)	a	24.88 (± 0.84)	a	24.90 (± 1.07)	a	0.998
Y12	Oct	25.26 (± 0.88)	a	25.48 (± 0.92)	a	25.14 (± 0.83)	a	25.24 (± 1.02)	a	0.887
	Nov	25.23 (± 0.64)	a	25.31 (± 0.81)	a	25.30 (± 0.61)	a	25.47 (± 1.28)	a	0.85
	Dec	23.60 (± 0.64)	a	23.68 (± 0.32)	a	23.80 (± 0.37)	a	23.76 (± 0.44)	a	0.802
	Jan	24.20 (± 0.32)	a	24.24 (± 0.16)	a	24.31 (± 0.19)	a	24.28 (± 0.23)	a	0.573
	Feb	24.81 (± 0.01)	a	24.80 (± 0.01)	a	24.81 (± 0.01)	a	24.81 (± 0.01)	a	0.638
	Mar	26.86 (± 1.25)	a	26.69 (± 0.64)	a	26.33 (± 0.76)	a	26.25 (± 0.82)	a	0.343
	Apr	25.90 (± 0.87)	a	26.06 (± 1.05)	a	25.79 (± 0.87)	a	25.96 (± 1.01)	a	0.946
	Average	24.84 (± 0.59)	a	24.87 (± 0.53)	a	24.75 (± 0.53)	a	24.82 (± 0.62)	a	0.738
	May	25.30 (± 0.64)	a	25.42 (± 0.50)	a	25.44 (± 0.60)	a	25.28 (± 0.59)	a	0.905
	Jun	24.48 (± 0.32)	a	24.41 (± 0.28)	a	24.47 (± 0.44)	a	24.54 (± 0.34)	a	0.884
	Jul	23.90 (± 0.26)	a	24.01 (± 0.32)	a	24.06 (± 0.28)	a	24.02 (± 0.28)	a	0.688
	Aug	23.88 (± 0.29)	a	23.87 (± 0.27)	a	23.88 (± 0.35)	a	23.86 (± 0.34)	a	0.999
	Sep	24.30 (± 0.22)	a	24.38 (± 0.23)	a	24.28 (± 0.20)	a	24.31 (± 0.22)	a	0.789
Y55	Oct	24.63 (± 0.20)	a	24.71 (± 0.20)	a	24.66 (± 0.24)	a	24.70 (± 0.23)	a	0.956

	Nov	24.97 (± 0.19)	a	25.05 (± 0.17)	a	25.05 (± 0.27)	a	25.09 (± 0.24)	a	0.705
	Dec	23.90 (± 0.35)	a	24.02 (± 0.22)	a	24.04 (± 0.28)	a	24.04 (± 0.26)	a	0.65
	Jan	24.64 (± 0.18)	a	24.73 (± 0.12)	a	24.78 (± 0.30)	a	24.70 (± 0.17)	a	0.561
	Feb	24.33 (± 0.19)	a	24.17 (± 0.28)	ab	23.96 (± 0.28)	b	23.96 (± 0.33)	b	0.016
	Mar	26.48 (± 0.77)	a	26.59 (± 0.81)	a	26.53 (± 0.81)	a	26.94 (± 0.87)	a	0.988
	Apr	24.98 (± 0.91)	a	25.00 (± 0.84)	a	25.02 (± 0.90)	a	25.10 (± 0.98)	a	0.992
	Average	24.65 (± 0.91)	a	24.70 (± 0.84)	a	24.68 (± 0.90)	a	24.71 (± 0.98)	a	0.99

Values are results from plot averages, NL is no litter, NLR is no litter and roots, NLRM is no litter, roots and mycorrhizae. SD is standard deviation, letters in each row represents relationship among collars where values with the same letter are not significantly different ($p < 0.05$) using Tukey HSD test.

Appendix 3D: Day-time soil moisture (%) for soil respiration partitioning collars at Y12 and Y55 site measured over the study period

Site	Month	Control		NL		NLR		NLRM		p - value
		Mean (± SD)		Mean (± SD)		Mean (± SD)		Mean (± SD)		
	May	—		—		—		—		
	June	5.89 (± 3.48)	a	3.89 (± 1.83)	a	3.67 (± 3.04)	a	2.89 (± 2.89)	a	0.171432
	Jul	4.33 (± 2.96)	a	2.22 (± 1.79)	a	2.44 (± 2.01)	a	2.89 (± 2.62)	a	0.255216
	Aug	3.33 (± 1)	a	3.11 (± 2.37)	a	2.89 (± 1.83)	a	3.44 (± 2.74)	a	0.944715
	Sep	6.33 (± 3.39)	a	3.89 (± 2.42)	a	5 (± 2.45)	a	3.89 (± 3.41)	a	0.263828
Y12	Oct	9.28 (± 1.31)	a	8.72 (± 2.46)	a	7.98 (± 1.81)	a	7.4 (± 2.18)	a	0.220845
	Nov	3.54 (± 3.6)	a	3.52 (± 3.65)	a	3.52 (± 3.39)	a	4.73 (± 5.9)	a	0.909339
	Dec	2.98 (± 1.82)	a	2.68 (± 1.17)	a	2.42 (± 0.57)	a	2.63 (± 0.92)	a	0.809269
	Jan	3.18 (± 1.59)	a	2.32 (± 1.33)	a	1.64 (± 0.79)	a	2.07 (± 1.1)	a	0.080402

	Feb	3.8 (± 2.45)	a	2.94 (± 2.25)	a	4.49 (± 2.69)	a	3.87 (± 2.66)	a	0.637779
	Mar	3.77 (± 2.11)	a	3.11 (± 1.63)	a	4.22 (± 2.78)	a	5.23 (± 4.43)	a	0.499114
	Apr	2.28 (± 0.87)	a	1.5 (± 0.74)	a	2.82 (± 2.42)	a	3.01 (± 3.08)	a	0.408883
	Average	4.43 (±2.23)	a	3.45 (±1.97)	a	3.74 (±2.16)	a	3.82 (±2.9)	a	0.123768
	May	—		—		—		—		
	June	3.56 (± 3.13	a	3.56 (± 2.7	a	2.11 (± 1.27	a	5.44 (± 5.85	a	0.301118
	Jul	2.11 (± 1.69	a	3.22 (± 2.33	a	1.44 (± 0.73	a	3.67 (± 2.96	a	0.11781
	Aug	5 (± 2.87	a	3.67 (± 2.35	a	3.11 (± 1.36	a	5 (± 3.46	a	0.327247
	Sep	6.67 (± 4.92	a	5.22 (± 4.47	a	4 (± 1.73	a	6.33 (± 3.32	a	0.451355
Y55	Oct	11.4 (± 3.49	a	9.78 (± 2.61	a	9.59 (± 3.26	a	9.09 (± 3.19	a	0.456507
	Nov	5.71 (± 3.41	a	5.42 (± 2.73	a	4.06 (± 3.08	a	5.98 (± 4.19	a	0.642552
	Dec	4.66 (± 2.32	a	3.56 (± 1.84	a	2.63 (± 1.48	a	3.49 (± 1.63	a	0.16329
	Jan	3.9 (± 2.63	a	3.26 (± 2.36	a	2.31 (± 1.46	a	3.02 (± 2.49	a	0.533873
	Feb	6.54 (± 3.41	a	6.13 (± 2.49	a	6.72 (± 2.06	a	6.17 (± 3.1	a	0.962349
	Mar	3.49 (± 1.66	a	2.9 (± 1.53	a	3.34 (± 2.22	a	4.46 (± 3.08	a	0.522775
	Apr	2.76 (± 1.04	a	3.08 (± 1.25	a	2.63 (± 1.27	a	3.02 (± 2.05	a	0.901296
	Average	5.07 (± 2.78	a	4.53 (± 2.42	a	3.81 (± 1.81	a	5.06 (± 3.21	a	0.489107

Values are results from plot averages, NL is no litter, NLR is no litter and roots, NLRM is no litter, roots and mycorrhizae. SD is standard deviation, letters in each row represents relationship among collars where values with the same letter are not significantly different ($p < 0.05$) using Tukey HSD test.

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Appendix 3E: Repeated measures analysis of variance (RMANOVA) results for seasonal variation in soil temperature and soil moisture for Y12 and Y55 site.

Variable	Site	Source	Sum of Squares	df	Mean Square	F	P-value
Soil temperature	Y12	Season	1.157	1	1.157	19.852	< 0.0001
		Error	1.923	33	0.058		
		Total	3.08	34	1.215		
	Y55	Season	0.011	1	0.011	0.204	0.655
		Error	1.762	33	0.053		
		Total	1.773	34	0.064		
Soil moisture	Y12	Season	65.297	1	65.297	101.228	< 0.0001
		Error	21.287	33	0.645		
		Total	86.584	34			
	Y55	Season	32.138	1	32.138	63.096	< 0.0001
		Error	16.809	33	0.509		
		Total	48.947	34			

Appendix 4A: Day-time average total soil respiration (g CO_2 m^{-2} hr^{-1}) for Y12 and Y55 site measured over the study period.

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Site		Month												Mean
							Nov							
							0.78							
	Max	2.98	1.70	2.23	1.36	2.15	2.13	2.91	1.33	1.28	1.46	1.81	1.64	—
Y12	Min	0.23	0.14	0.35	0.11	0.37	0.56	0.26	0.13	0.14	0.21	0.06	0.31	—
	Statistic	May	Jun	Jul	Aug	Sep	Oct		Dec	Jan	Feb	Mar	Apr	
	m													
	Mean	1.18	0.80	0.74	0.61	1.02	1.06		0.44	0.51	0.57	0.66	0.68	0.75
	SD	0.57	0.38	0.24	0.35	0.43	0.43	0.50	0.25	0.25	0.24	0.33	0.30	0.23
	CV (%)	48.73	48.19	32.80	57.01	42.09	40.31	63.50	57.28	49.43	42.34	50.12	43.51	47.94
	Mean	0.82	0.92	0.79	0.69	0.94	0.89	0.65	0.64	0.52	0.73	0.69	0.66	0.75
	Max	3.38	1.74	1.74	1.96	2.47	1.75	1.34	2.76	2.05	1.70	1.44	2.08	—
Y55	Min	0.20	0.34	0.37	0.26	0.09	0.28	0.30	0.16	0.10	0.20	0.03	0.30	—
	SD	0.54	0.34	0.39	0.32	0.56	0.40	0.28	0.45	0.34	0.29	0.35	0.37	0.13
	CV (%)	66.46	36.87	49.71	46.42	59.04	44.79	42.74	70.98	64.34	40.00	49.69	55.62	52.22

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ation, and CV is coefficient of variation. *P*-value tested with Student's *t*-test.

Appendix 4B: Day-time soil moisture respiration (g CO_2 m^{-2} hr^{-1}) for partitioning collars at Y12 and Y55 site measured over the study period.

Site	Month	Control		NL		NLR		NLRM		p - value
		Mean (± SD)		Mean (± SD)		Mean (± SD)		Mean (± SD)		
	May	0.94 (± 0.49)	a	0.73 (± 0.30)	ab	0.43 (± 0.27)	b	0.37 (± 0.35)	b	0.0173
	June	0.86 (± 0.36)	a	0.81 (± 0.77)	a	0.35 (± 0.17)	a	0.39 (± 0.30)	a	0.0609
	Jul	0.67 (± 0.36)	a	0.54 (± 0.16)	ab	0.36 (± 0.13)	b	0.31 (± 0.15)	b	0.0067
	Aug	0.62 (± 0.19)	a	0.48 (± 0.12)	ab	0.36 (± 0.13)	b	0.29 (± 0.14)	b	0.0003
	Sep	0.98 (± 0.39)	a	0.76 (± 0.16)	ab	0.47 (± 0.14)	bc	0.37 (± 0.26)	c	< 0.0001
Y12	Oct	1.02 (± 0.41)	a	0.82 (± 0.13)	ab	0.45 (± 0.30)	bc	0.37 (± 0.23)	c	0.0001
	Nov	0.70 (± 0.48)	a	0.51 (± 0.17)	a	0.42 (± 0.16)	a	0.35 (± 0.09)	a	0.0640
	Dec	0.36 (± 0.14)	a	0.36 (± 0.06)	a	0.29 (± 0.08)	ab	0.22 (± 0.07)	b	0.0094
	Jan	0.43 (± 0.21)	a	0.37 (± 0.12)	ab	0.27 (± 0.09)	ab	0.22 (± 0.08)	b	0.0098
	Feb	0.59 (± 0.17)	a	0.55 (± 0.10)	ab	0.17 (± 0.17)	b	0.29 (± 0.21)	b	0.0034
	Mar	0.51 (± 0.44)	a	0.48 (± 0.22)	a	0.43 (± 0.29)	a	0.23 (± 0.12)	a	0.3078
	Apr	0.65 (± 0.30)	a	0.55 (± 0.15)	ab	0.36 (± 0.08)	bc	0.27 (± 0.12)	c	0.0005
	Average	0.69 (± 0.21)	a	0.58 (± 0.16)	b	0.37 (± 0.09)	c	0.31 (± 0.06)	c	< 0.0001

	May	0.86 (± 0.37)	a	0.63 (± 0.44)	ab	0.26 (± 0.14)	b	0.29 (± 0.05)	b	0.0004
	Jun	0.96 (± 0.37)	a	0.87 (± 0.22)	a	0.38 (± 0.05)	b	0.28 (± 0.12)	b	< 0.0001
	Jul	0.53 (± 0.18)	a	0.44 (± 0.15)	ab	0.28 (± 0.09)	bc	0.22 (± 0.06)	c	< 0.0001
	Aug	0.70 (± 0.19)	a	0.57 (± 0.26)	ab	0.35 (± 0.15)	bc	0.23 (± 0.07)	c	< 0.0001
	Sep	0.60 (± 0.39)	abc	0.82 (± 0.36)	a	0.41 (± 0.10)	b	0.30 (± 0.14)	b	0.0040
Y55	Oct	0.73 (± 0.40)	a	0.68 (± 0.37)	ab	0.41 (± 0.16)	ab	0.31 (± 0.09)	b	0.0102
	Nov	0.82 (± 0.32)	a	0.68 (± 0.31)	ab	0.37 (± 0.10)	bc	0.32 (± 0.09)	c	0.0003
	Dec	0.55 (± 0.15)	a	0.46 (± 0.14)	a	0.29 (± 0.16)	b	0.28 (± 0.07)	b	0.0002
	Jan	0.49 (± 0.21)	a	0.44 (± 0.14)	a	0.31 (± 0.14)	ab	0.17 (± 0.11)	b	0.0018
	Feb	0.80 (± 0.18)	a	0.45 (± 0.09)	b	0.34 (± 0.18)	b	0.29 (± 0.09)	b	< 0.0001
	Mar	0.50 (± 0.30)	a	0.47 (± 0.12)	a	0.30 (± 0.19)	a	0.31 (± 0.10)	a	0.0587
	Apr	0.46 (± 0.21)	a	0.36 (± 0.21)	ab	0.17 (± 0.20)	b	0.31 (± 0.09)	b	0.0027
	Average	0.67 (±0.17)	a	0.57 (± 0.16)	b	0.32 (± 0.07)	c	0.27 (± 0.05)	c	< 0.0001

Values are results from plot averages, NL is no litter, NLR is no litter and roots, NLRM is no litter, roots and mycorrhizae. SD is standard deviation, letters in each row represents relationship among collars where values with the same letter are not significantly different ($p < 0.05$) using Tukey HSD test.

Appendix 4C: Day-time averages of component soil respiration (g CO_2 m^{-2} hr^{-1}) at Y12 and Y55 site measured over the study period.

Month/Component respiration Site												Mean
Statistic	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr

		Root-and-rhizosphere respiration												
Y12	Mean													
	SD	0.51	0.34	0.18	0.17	0.32	0.37	0.21	0.09	0.11	0.33	0.21	0.19	0.25
		0.34	0.23	0.11	0.02	0.2	0.28	0.23	0.06	0.08	0.16	0.22	0.09	0.12
	Mean	0.63	0.54	0.22	0.31	0.41	0.48	0.25	0.19	0.2	0.24	0.24	0.5	0.35
Y55														
	SD	0.47	0.23	0.12	0.21	0.36	0.23	0.16	0.09	0.13	0.18	0.23	0.38	0.15
	p - value	0.6058	0.1526	0.4589	0.1153	0.2426	0.8293	0.0825	**0.0273**	0.0873	0.9174	0.7373	0.5728	0.0963
		Mycorrhizal respiration												
Y12	Mean	0.32	0.15											
	SD	0.16	0.03	0.1	0.11	0.17	0.35	0.14	0.09	0.08	0.21	0.25	0.14	0.18
				0.1	0.08	0.08	0.19	0.1	0.06	0.06	0.22	0.31	0.07	0.09
	Mean	0.11	0.17	0.08	0.17	0.13	0.19	0.1	0.32	0.11	0.13	0.04	0.22	0.15
Y55														
	SD	0.1	0.09	0.05	0.08	0.17	0.2	0.1	0.16	0.18	0.02	0.04	0.2	0.07
	p - value	**0.0434**	0.672	0.5422	0.2503	0.5739	0.0592	0.6277	0.9292	**0.003**	0.0561	0.6392	**0.0293**	0.4055
		Litter respiration												
Y12	Mean SD	0.52	0.47	0.26	0.17	0.4	0.48	0.18	0.13	0.13	0.31	0.18	0.22	0.29
		0.31	0.24	0.15	0.15	0.25	0.43	0.06	0.15	0.12	0.44	0.12	0.22	0.14
	Mean	0.29	0.32	0.22	0.16	0.55	0.25	0.17	0.17	0.4	0.22	0.18	0.13	0.26
Y55														
	SD	0.18	0.24	0.16	0.14	0.57	0.23	0.09	0.07	0.22	0.19	0.06	0.04	0.12
	p - value	0.107503	0.290896	0.6354	0.9643	**0.0381**	0.8258	0.5841	0.5959	0.5348	0.6201	0.7621	0.6771	0.5561
		Soil organic matter respiration												
	Mean	0.42	0.43	0.31	0.29	0.37	0.37	0.35	0.22	0.22	0.33	0.25	0.27	0.32
Y12	SD	0.34	0.28	0.15	0.14	0.26	0.23	0.09	0.07	0.08	0.2	0.08	0.12	0.07
	Mean	0.29	0.28	0.22	0.23	0.31	0.32	0.28	0.17	0.29	0.31	0.21	0.3	0.27
Y55														
	SD	0.05	0.12	0.06	0.07	0.09	0.09	0.07	0.11	0.09	0.1	0.09	0.14	0.05
	p - value	0.2876	0.1418	0.1066	0.2463	0.5126	0.4299	0.4298	0.0809	0.2417	0.5395	0.2467	0.3077	**0.0497**

Values are results from daily plot averages, SD is standard deviation. *P*-value tested with Student's *t*-test.

Appendix 4D: Repeated measures analysis of variance (RMANOVA) results for seasonal variation in total and component soil respiration at Y12 and Y55 site for the study period.

Total soil respiration

Site	Source	Sum of Squares	df	Mean Square	F	P-value
Y12	Season	1.399	1	1.399	77.325	< 0.0001
	Error	0.597	33	0.018		
	Total	1.996	34			
Y55	Season	0.257	1	0.257	10.173	0.0031
	Error	0.833	33	0.025		
	Total	1.089	34			
Root-and-rhizospher respiration						
Y12	Season	0.088	1 8	0.088	18.583	0.0026
	Error	0.038		0.005		
	Total	0.127	9			
Y55	Season	0.158 0.083	1	0.158 0.010	15.153	0.0046
	Error		8			
	Total	0.241	9			
Mycorrhi al espirati on						
Y12	Season	0.001	1	0.0014	0.230	0.6445
	Error	0.050	8	0.0063		
	Total	0.052	9			
Y55	Season	0.003	1 8	0.0031	0.630	0.4501
	Error	0.039		0.0049		
	Total	0.042	9			
litter respiration						
Y12	Season	0.148 0.032	1	0.148 0.005	32.747	0.0007
	Error		7			
	Total	0.179	8			
Y55	Season	0.002	1	0.002	0.212	0.6575
	Error	0.059	8	0.007		
	Total	0.060	9			
Soil organic matter respiration						
	Season	0.040 Y12	1	0.040	3.731	0.0895
Error 0.085			8	0.011		

	Total	0.125		9				
	Season	0.001	Y55	1	0.001	0.001	0.792	0.3995
Error	0.006			8				
	Total	0.006		9				

Appendix 5: One-way ANOVA results for annual respiration estimates.

Site	Source of Variation	SS	df	MS	F	P-value
Y12	Between Groups	1.103	3	0.368	8.821	< 0.0001
	Within Groups	13.427	322	0.042		
	Total	14.530	325			
Y55	Between Groups	1.593	3	0.5310	13.731	< 0.0001
	Within Groups	12.647	327	0.0387		
	Total	14.240	330