Study of the effect of temperature on the cycling of carbon in a forest ecosystem at Mount Taranaki

A thesis presented in partial fulfilment of the requirements for the degree of

Master of Science

in

Soil Science

School of Agriculture and Environment

Palmerston North, New Zealand

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2020

Abstract

Soil organic matter (OM) represents one of the largest reservoirs of carbon (C) on the global scale. It is therefore crucial to understand the potential response of these C stocks to global warming. Global mean surface temperature is likely to increase by between 1.4 °C and 3.1 °C by the end of the 21st century (2081–2100), relative to 1986–2005 range, and it is anticipated that any warming-induced C emissions from soils will further drive planetary warming. However, there is disagreement on the potential feedbacks of soil organic C to climate warming, due to the complexity of the relationship between climate warming and soil C. The objective of this study was therefore to assess how changes in temperature affects the cycling of soil OM in a thermo-sequence at the Egmont National Park in Taranaki. Soil samples were collected at four sites (in a transect of increasing altitudes, ranging from 512 m to 1024 m asl) down to 40 cm depth, at depth increments of 5 cm, using PVC pipes of 5 cm Ø. Additional soil samples were taken for a general chemical characterisation of the soils at time 0. The soil columns were incubated for 190 days at four different temperatures (5°C, 15°, 25°C and 35°C) using a 0.25 M NaOH solution to trap CO_2 with soil moisture maintained at field capacity. A three-pool C model was used to determine the rate of C decay in the C fractions/pools. The results showed that, in general, altitude did not have a significant effect on either C stocks or cumulative C efflux at the end of the laboratory incubation. Cumulative C efflux was ~3 times larger (significant at $P<0.05$) at the highest temperature (e.g., 0.015 t C/ha/day for topsoil layer) compared with the lowest temperature (0.005 t C/ha/day for topsoil layer). At all temperatures and sites, the topsoil layer had the largest C efflux (ranging from 0.015 to 0.005 t C/ha/day) compared with the deeper layers (averaged between 0.006 to 0.002 t C/ha/day). The Q_{10} values (averagely 1.47-1.35) revealed that all soil layers were temperature sensitive. All three C pools considered (fast, intermediate, slow) were temperature sensitive, though C efflux in the slow pool was very small (< 0.00006 t C/ha/day). We attributed the higher C efflux in the topsoil to the presence of more labile C enriched in necromass, weaker interaction of organic ligands with mineral components and high microbial abundance. Our findings showed that a rise in temperature enhanced the decomposition of soil OM even at the deepest layer, where mineral protection is largest. Also, the organic C at all C pools, soil layers, and altitudes were shown to be temperature sensitive.

Acknowledgements

Firstly, I would like to dedicate this work to my lovely mother whose prayers, support, advice and guidance has brought me this far. Her perseverance to help me climb the academic ladder despite all obstacles is invaluable. I really appreciate all her efforts.

Secondly, I would like to express my deepest gratitude to all my supervisors, Professor Marta Camps-Arbestain, Dr Miko Kirschbaum, Dr Gabor Kereszturi and A/Prof. Alan Palmer for their enormous support to the success of this work. Their advice, assistance and mentorship helped me acquire a lot of knowledge not only in this subject area but also about the world at large. I particularly want to thank Professor Marta whose door was always open for my questions and guidance to research/writing. Her patience to help me understand every part of the work is something I really admired. She steered me in the right direction and working hard for this research work to be published. I also thank Dr Miko for teaching me how to develop a statistical model for C analyses.

Thirdly, I would also like to thank Idri Hastuty Siregar for her immense support during the soil incubation and chemical analysis of the soil samples. Not forgetting Ian Furkert for his support during preparation of solutions for chemical analysis and calibrations.

Fourthly, studying in New Zealand would not have been a reality without the financial support from the Ministry of Foreign Affairs and Trade (MFAT). I therefore thank the Ministry for such assistance. Many thanks to the Massey University International Student Support for their pastoral care for academic and non-academic issues throughout my study period in Massey University.

Lastly, am grateful to all my friends especially Ben Poulton, Romana Mbinya, Yahaya Amanor Jebril, Obvy Moyo and Abena Konadu Oppong for their help and support throughout my studies. They were always ready to share information and provide support.

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1.0 Chapter 1: Introduction

1.1 Background

The world soil C pool (to a depth of 2 m) of 2500 Gt represents the largest terrestrial C reservoir, 3.3 times the size of the atmospheric pool and 4.5 times the size of the biotic pool (Batjes, 1996; Lal, 2004). About 60 Gt soil C is released to the atmosphere annually through soil respiration (i.e., decomposition), which is approximately replenished by the same amount through new litter influx from senescing plant leaves, roots or other carbon sources (Paul, 2014). Given the importance of soil C in the global C cycle, a global warming effect on the balance of C inputs and outputs could have a great effect on terrestrial C under changing climate (Davidson & Janssens, 2006). Soil could become a C source instead of a C sink, as has happened during the last century due to unsustainable soil management practices (Corinne Le Quéré et al., 2015). If accelerated decomposition outpaces the potential C input from enhanced plant growth, considerable amounts of C could be lost to the atmosphere, causing further planetary warming (Crowther et al., 2016). The increase of global mean surface temperature by the end of the 21st century (2081–2100) relative to 1986–2005 is likely to be 1.4°C to 3.1°C under Representative Concentration Pathways 6.0 (Pachauri et al., 2014). This extrapolation would suggest that warming could drive the net loss of approximately 55±50 Gt C from the upper soils horizon (Crowther et al., 2016). This is because the Representative Concentration Pathways 6.0 assumes that soil organic matter (OM) decomposition outpaces the gain through enhanced decomposition. The temperature sensitivity of decomposition has recently received considerable attention, including several high-profile publications supporting opposing views (Giardina et al., 2014; Ise & Moorcroft, 2006; Meyer et al., 2018; Qin et al., 2019). Yet, the efforts to quantify the underlying temperature-sensitive processes have not been adequate for predicting the land C-climate feedback (Kirschbaum, 2000, 2010).

The relationship between soil OM lability and temperature sensitivity are complex (Giardina & Ryan, 2000). In part because of the occurrence of various acclimation processes, including microbial adjustments at cellular and community levels, and potential changes in litter and soil-C quality (Giardina & Ryan, 2000). Soil respiration seems to respond positively to warming, as many studies have documented short-term (annual to decadal) increases in soil C decomposition with increased temperature (Kirschbaum, 2000). Net primary production tends to increase with warming, in the absence of other limiting factors (e.g., water limitations), with a corresponding increase in the amount of plant-derived C available below-ground. Temperature sensitivity of soil OM decomposition is also influenced by its chemical

composition. This increases with decreasing soil OM lability (Conant et al., 2008), and chemical interactions with minerals (Shen et al., 2018a). Further, increased detrital production could stimulate soil C decomposition and accelerate turnover of soil organic C (Sayer et al., 2011). A net balance in such processes needs to be evaluated from an ecosystem perspective.

Studies on the effect of temperature on the C cycle are challenged by the fact that thermo-sequences generally co-vary with other environmental properties. The Taranaki region offers a unique opportunity to study the C stocks and fluxes in a whole forest ecosystem, as there is a 5 °C median annual average temperature gradient under a common precipitation regime (~2000 mm annual precipitation) (Figure 3.2). Moreover, soils of this volcanic region are Andosols, which are characterized by having a high content of short–range ordered constituents (e.g., allophane, imogolite, ferrihydrite) and high soil OM contents (Shen et al., 2018a). The high C stocks are related to greater ability of these constituents to interact with soil OM. The interaction leads to formation of organo-mineral complexes and offering a greater protection against decomposition than soils in which other clay-type constituents are present. However, given their large C stocks, they might have a greater lability than other soils when subject to environmental changes. As the influence of increasing temperature on the stability of soil OM in these soils with abundant organo-mineral complexes is not yet understood, studies are needed to ascertain the relationship between temperature and preservation of soil OM in these soils, such as volcanic areas. This will help to map out ways to mitigate climate change or adapt to it, especially in New Zealand. The distinct thermo-sequence across the gradient of the soils in the Egmont National Park with andic properties makes it suitable for studying the dynamics of soil OM cycling within a temperature gradient.

1.2 Main objective

The goal of the study was to assess the influence of temperature on the cycling of soil OM in a thermo-sequence under native forest at the Egmont National Park in Taranaki.

1.3 Specific objectives

i) To assess soil physicochemical properties at the different sites (and depths) of the thermo-sequence (annual mean temperatures ranging from 6.7 to 9.9°C).

ii) To assess the lability of soil OM at the different sites (and depths) of the thermo-sequence when incubated at different temperatures in the laboratory (incubation temperatures ranging from 5 to 35 °C).

1.4 Hypotheses

i) The soil OM at the lowest altitude will have a smaller susceptibility to increasing temperature, given that it is dominated by a more decomposed and less stratified OM, as opposed to the soil OM at the highest altitude.

ii) When incubated in the laboratory, a rise in temperature under favourable moisture content will enhance microbial activity at all sites and thus the rate of soil OM decomposition.

iii). The effect of temperature on soil OM decomposition should be greatest in the topsoil (compared with deeper layers) and at the highest altitude (compared with lower altitudes).

iv) Out of the three organic C pools (fast, intermediate, slow), as estimated by a three pool C model, the fast pool will be most sensitive to temperature, followed by the intermediate and the slow pool.

2.0 Chapter 2: Literature Review

2.1 Soil Organic Matter

2.1.1 Background

Brady and Weil (1999) define soil organic matter (OM) as plant and animal residues at different stages of decomposition. This includes cells and tissues of soil organisms, and decomposed substances that build up when the rate of decomposition is slower than the rate at which soil OM is added. Soil organic matter contains thrice as much carbon as found in the atmosphere or terrestrial flora, making it the largest carbon reservoir in terrestrial ecosystems (von Lützow & Kögel-Knabner, 2009). This means that releasing and converting carbon in soil OM to CO_2 will have a substantial impact on the greenhouse gas effect (Lehmann & Kleber, 2015).

Soil organic matter influences the physicochemical and biological properties of the soil, hence improves soil functions. The effects of soil OM on the physical, chemical and biological properties of the soil include:

i) Contributes to the cation exchange capacity (the amount of negative charges) of the soil, as this is mostly controlled by the presence of colloidal organic matter and clay particles (Kaiser et al., 2008; Tate, 1987).

ii) Organic matter improves the structure of the soil through increasing of pore volume, which increases the soil water retention, the infiltration rate of the soil and the rate of gas exchange. Soil OM improves soil structure by bonding mineral particles into stable aggregates (Funderburg, 2001; Oades, 1984). The improvement of soil structure is facilitated by microbial transformation through decomposition of soil OM (Tate, 1987). There are other factors such as type of soil (determined by the interaction of soil forming factors: climate, parent material, slope, biota, and time elapsed since formation), and management strategies that affect the structure of the soil, aside from soil OM (Kay, 2018).

iii) Plant productivity has strongly been associated with soil OM content (Bauer & Black, 1994). However, there is now some debate on this, as soils that are correctly fertilized with inorganic fertilizers have been shown to give similar yield to soils fertilized with organic amendments. Still a higher soil OM content improves the resilience of the agronomic systems against adverse environmental events (Chen et al., 2018). Organic matter is a nutrient reservoir for plant growth and contributes to nutrient retention.

2.1.2 Sources of soil organic matter

Organic detritus reaches the soil as parts of plants and animal remains. Crop residues (including plant roots), animal manures, green manures, dead animals, microorganisms, compost, and organic fertilizers are the major sources of soil OM. The composition of soil OM includes: (1) carbohydrates (sugars, starches, cellulose, hemicellulose, gums, pectin, etc.), (2) N compounds (proteins, amino acids, amines, etc.) (3) organic acids, (4) lignin, (5) fats and oils, waxes, resins, (6) alcohols, aldehydes, ketones, (7) compounds with ring or cyclic structures like phenols and tannins, (8) alkaloids and compounds with organic bases (purine, pyridine, etc.), and (9) other essential substances (like antibiotics, pigments, vitamins, enzymes and auxins) present in small quantities. The major elements contained in soil OM are carbon (C), hydrogen (H), oxygen (O), nitrogen (N), sulphur (S) and phosphorus (P) (Paul, 2016).

2.1.3 Soil organic and inorganic carbon and their stocks

Soil carbon is grouped under two components, namely, soil organic carbon (SOC) and soil inorganic carbon (SIC) (Lal, 2007). Soil organic carbon is a constituent of soil OM whereas SIC is present in carbonate minerals (e.g., calcite, dolomite, aragonite, and siderite). Soil C stocks are estimated to be 2,500 Pg C, consisting of 1,550 Pg C of SOC and 950 Pg C of SIC (Dungait et al., 2012). The quantity and behavior of SOC is highly influenced by the properties of the soil, the location of the landscape, the nature of the terrain, temperature and rainfall (Lal, 2007). In an undisturbed (natural) system, SOC ranges from 40 to 400 Mg C/ha (Post et al., 1982). The conversion of natural vegetation to agricultural systems can cause a depletion of this SOC amount. This can be 50 to 75% within 5 to 20 years in tropical soils, and 25 to 50% in temperate soils within 20 to 50 years; depending on the intensity of the depletion (Lal, 2007). Decomposing SOC contributes to increasing CO_2 concentration in the atmosphere leading to global warming.

2.1.3.1 Labile SOC

Labile organic carbon is the fraction of carbon with the shortest turnover rate (mostly less than 5 years). It is most abundantly found within the top 10 cm of the soil profile and easily degradable, so it supports microbial growth (Hoyle & Murphy, 2006; Zou et al., 2005). The oxidation of labile C has a strong influence on the soil CO_2 flux to the atmosphere (Coleman & Crossley Jr, 1996). Labile organic carbon may constitute a small part of the total SOC.

However, it is the most active pool, and used as an indicator for assessing the quality of soil as it is very responsive to land use changes and management (Cai et al., 2016; Shen et al., 2018b). Chen et al. (2019) proposed that an ecosystem capable of maintaining a high amount of labile C is the best system for SOC sequestration. He further stated that, if an ecosystem can maintain a high turnover of labile SOC, then that system is able to store a lot of the newly formed labile SOC. Soil microorganisms mostly derive their energy from labile carbon. Nutrient cycling, bioavailability of plant nutrients, productivity and environmental resilience have also been linked to labile carbon (Bongiorno et al., 2019; Chantigny, 2003; Haynes, 2005). Reducing tillage practices and maintaining a high amount of organic matter inputs has been found to increase labile C in the soil while enhancing the cycling of C and N, and soil aggregation (Bongiorno et al., 2019; Cooper et al., 2016; Panettieri et al., 2015).

2.1.3.2 Preserved SOC

Preserved OM (C) is a complex mixture of organic compounds with a long-turnover time, which is mostly associated with microbial-derived soil OM. The preserved OM is protected from decomposition either physically in soil aggregates or chemically too complex to be reached by microorganisms (Schmidt et al., 2011). However, there is an argument that the preserved soil OM can break down. This is based on the presence of easily accessible and readily decomposable molecules in even the oldest SOC fraction. Preserved organic C plays an important role in terms of nutrient cycling. It is considered a nutrient reservoir, as it stores soil nutrients for a long period. Preserved SOC also improves soil aggregation and stability, increasing the CEC for nutrient retention in soil (Bot & Benites, 2005).

2.1.3.3 Inert SOC

Inert SOC is associated with carbonized material and makes up a very small portion of SOC. The chemical structure of charred material makes it difficult to decompose in the short- and mid-term as most microbes lack suitable enzymes to break it down. Using the radiocarbon age of charred material and models, such as the RothC model, inert SOC has been found to last more than 50,000 years (Coleman & Jenkinson, 1996; Jenkinson, 1990; Sanderman et al., 2016).

2.2 Organic matter dynamics in the soil

The soil is constantly changing in response to changes in the environment. Many components of the soil undergo changes but over different time spans. The composition of the soil solution can change very quickly (i.e., in seconds) and the microbial communities of the soil can change in hours, days or weeks, whereas the mineralogy of the soil can change over decades or thousands of years (Janzen et al., 1997). Changes in environmental factors or in their interaction with other factors, affect the functions of the soil. Just as the soil is responsive to external factors, so is soil OM (Nogueira et al., 2016). For example, the physically-unprotected soil OM fraction is very responsive to land-use changes (Marin-Spiotta et al., 2009). This means that soil OM is variable and always acts according to external influences. The resultant interaction affects ecosystem functioning, soil quality, and fertility (Basso et al., 2011; Paul & Collins, 1997). Even though some of the indicators of soil quality are stable, others can quickly change in response to anthropogenic activities (Janzen et al., 1997; Loss et al., 2014). Any activity that affects the proportionality between net C primary production (NPP) and C decomposition affects the content of the OM in the soil. For instance, in early stages of ecosystem development, net production exceeds decomposition through high litter fall, leading to carbon accumulation. However, as the ecosystem matures, net C storage approaches zero due to a balance between NPP and decomposition (Chen et al., 2019; Janzen et al., 1997).

The dynamism of soil OM is driven by substrate quality, soil biota, soil aggregation, soil matrix, presence of bridging cations, as well as the chemical composition of the soil OM. These are influenced by the type of soil, the climatic conditions, the land-use system, and the management practices. These factors do not only have an influence on the soil OM quality and quantity but also significantly affect the microbial community structure and the functions of the decomposers (Feller & Beare, 1997; Paul et al., 2015).

The determination of soil OM dynamics can best be achieved by integrating laboratory incubations, extending experimental periods, determining the amount and characterising of ^{13}C or ^{15}N, as well as ^{14}C dating. To appreciate changes in soil OM, the effects of divergent land-use systems, climate and pedology can be studied through fractionation methods, the characterisation of soil OM fractions, and determination of turnover rates of the soil OM fractions (Deng et al., 2016a; Paul, 2016).

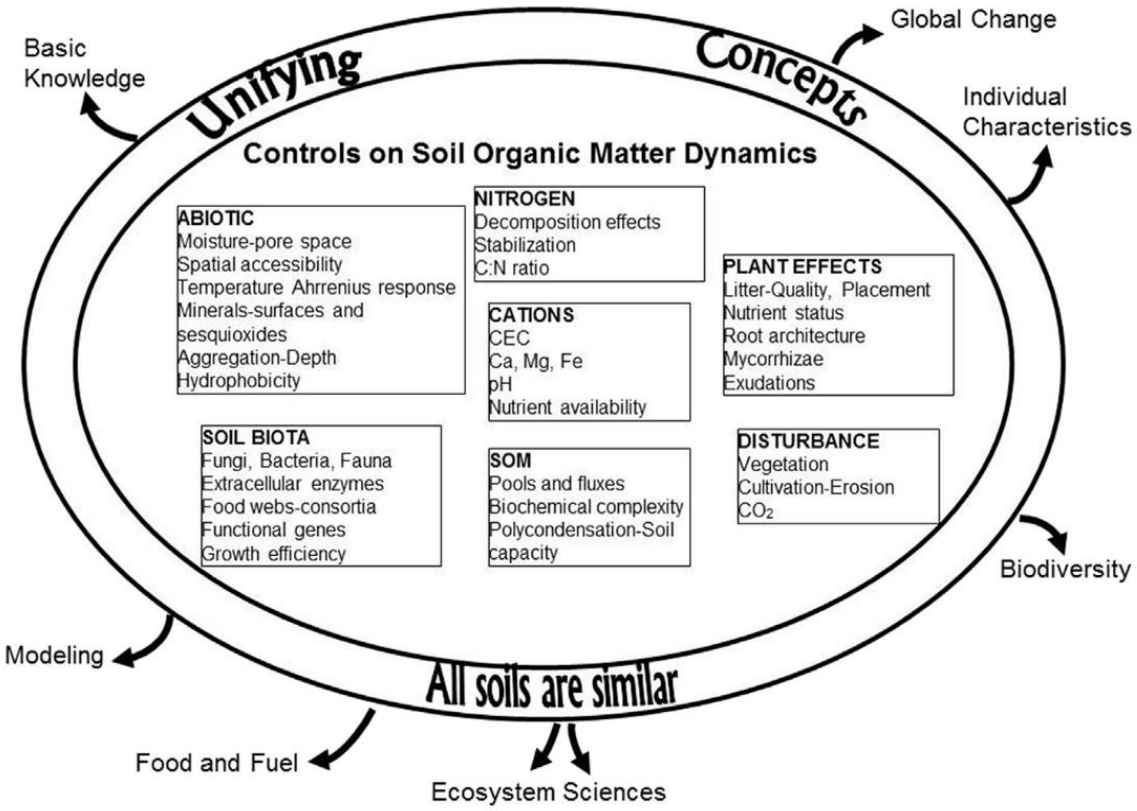

Figure 2. 1: Collective and integrative factors controlling soil OM formation and dynamics (Paul, 2016)

2.3 Soil organic matter decomposition

Soil OM decomposition is a process whereby the complex mixture of organic molecules from OM detritus are transformed into simpler organic and inorganic molecules through biological and biochemical processes (Juma, 1999). The natural process is facilitated by the quality and the amount of the soil OM present. Likewise, soil microorganisms' abundance and environmental conditions of the environment, such as temperature, moisture, and soil type also facilitate the process (Brussaard, 1994; Chapin III et al., 2011). Decomposition plays a very important role in ecosystem functioning and it is the major component of soil nutrient cycling. Through the decomposition of soil OM, nutrients such as N, P and S, become available to plants (Bot & Benites, 2005). These nutrients are often locked up in the tissues of dead organic matter and only become available to the soil through decomposition (Guenet et al., 2012). For this reason, decomposition serves as an indicator of soil health and quality. Organisms that breakdown macromolecules into simpler fractions are called decomposers. Each decomposer

has a specific role and type of organic material it can decompose. However, their collective interactions and activities are key to the nutrient cycling processes (Bot & Benites, 2005).

2.3.1 Process of soil organic matter decomposition

Organic detritus is made up of organic C macromolecules from plant, animal, and microbial tissues. Carbon atoms are interconnected within these organic molecules. The chains of carbon atoms, which can have varying amounts of nutrients attached, form simple sugars, amino acids, and more complex organic C rings. The decomposition process of some macromolecules can be faster than others. This is influenced by the chemical composition of the material and type of bonding (Bot & Benites, 2005). For example, sugars, starches and proteins decompose at a fast rate. Cellulose, fats, waxes, and resins, on the other hand, decompose at a relatively slower rate (Bot & Benites, 2005; Paul, 2016). Originally, lignin was thought to decompose slowly but it is now known that it decomposes at a relatively fast rate as long as the system is aerobic (Schellekens et al., 2015). Non-complex organic molecules stay in the soil for only a short period of time since they are easily consumed by organisms (Bot & Benites, 2005).

Both abiotic and biotic decomposition occurs, yet the biotic pathway is the most important. In the abiotic process, decomposition occurs through mechanical forces, such as those resulting from freezing or thawing, drying or wetting cycles, or even through the effect of light (Wetterstedt, 2010; Zepp et al., 2007). The biotic decomposition of soil OM is mainly controlled by bacteria and fungi since they make up approximately 95% of the decomposers biomass and soil respiration (Chapin III et al., 2011; Persson et al., 1980). Some molecules are too big and insoluble to be broken down by microbes during the decomposition process. For this reason, some microbes secrete extracellular enzymes to start the decomposition process.

Organic detritus, through decomposition, undergo physical fragmentation and chemical alteration. Physical fragmentation is the stage of decomposition where detritivores break down fresh detritus into smaller particles they can feed. As they feed, these detritivores create favourable conditions on the surface of the detritus for microbial colonization. During this process, the detritivores also mix the decaying detritus with soil particles. Though the presence and abundance of detritivores affect the rate of decomposition in both temperate and tropical ecosystems, their influence become insignificant to decomposition where the process is constrained by moisture and temperature (Chapin III et al., 2011; Wall et al., 2008). The chemical alteration is mainly controlled by soil microbes even though some activities occur

without microbial intervention. Soil microbes produce extracellular enzymes to degrade soil OM into water-soluble forms so that they can get access to it through depolymerisation (Li et al., 2015). The extracellular enzymes break down the soil OM through hydrolytic or oxidation processes. The depolymerisation reaction is sensitive to temperature (Conant et al., 2011).

2.3.2 Mechanisms of soil organic matter preservation

Preservation of soil OM has become an important issue in recent times due to its potential to increase C storage and thus contribute to mitigating greenhouse gas emissions (Rabbi et al., 2010). The preservation of soil OM is also important for agriculture production since it is a major determinant of the soil functions (Lal, 2009; Powlson et al., 2012). Current studies are focusing on mechanisms to preserve soil OM to reduce CO_2 emissions into the atmosphere while contributing to other soil functions (Rabbi et al., 2010).

Soil OM can be preserved through physical protection, which impedes the contact of decomposers/enzymes and the substrate; or chemical protection, which occurs through the interaction of soil mineral particles with the substrate or biochemical protection associated with charred materials (Mikutta et al., 2006; Plaza et al., 2013).

2.3.2.1 Physical protection

Physical protection is the process whereby soil OM is occluded from decomposition by forming a barrier to prevent decomposers and their enzymes from access to the organic substrate. This can also involve the slowdown of oxygen diffusion due to the presence of water (Plaza et al., 2013). The position of soil OM within stable aggregates can prevent microbes from gaining access to them. Physical protection is larger in micro-aggregates than in macro-aggregates. Therefore, changes in land-use or management activities have little or no influence on microaggregate stability, compared with macroaggregate, which is somewhat responsive (Matus et al., 2014). This also explains why Allophanic soils, with high abundance of microaggregates, have high ability to preserve soil OM (Chevallier et al., 2010; Woignier et al., 2008). The type of soil and the content of clay also influences physical protection. Physical protection of soil OM increases as the clay content in the soil increases (Franzluebbers & Arshad, 1997). The influence of clay type on soil OM protection differs with the type of clay. For example, 2:1 clay minerals like montmorillonite and vermiculite with high CEC and larger specific surface, have greater binding ability compared to those with less CEC and smaller

specific surface area like the illite (Greenland, 1965), as cited in Six et al. (2002b), or kaolinite (Fissore et al., 2016).

2.3.2.2 Chemical protection

The adsorption of soil OM to mineral surfaces makes decomposition a challenge as more effort is needed by the microbes to break down the existing bonds (such as ligand exchange, polyvalent cation bridges, H-bonding and van der Waals forces) (Kaiser & Guggenberger, 2003; Oades, 2013). Allophane and oxy-hydroxides of Fe and Al are short-ranged structural order constituents with a large specific surface area and broken end bonds which attract soil organic matter and chemically protect soil OM from rapid decomposition (Kögel-Knabner et al., 2008; Wagai et al., 2015). The association of soil OM with these inorganic surfaces and metal cations generate organo-mineral complexes that resist to microbial decomposition. The organo-mineral complex is described as a discrete zonal sequence. It looks like an "onion-type" shape where the magnitude of the bond, as well as the residence time declines as it moves farther away from the mineral (Hagerty et al., 2014; Kleber et al., 2015). Interestingly, the organic matter that becomes chemically protected is microbially-derived (Verde et al., 2008).

2.3.2.3 Biochemical protection

Biochemical protection is mostly associated with charred materials which contain condensed aromatic C produced from the combustion of vegetation/fossil fuels, and weathering of rocks, especially graphitic rocks (Nguyen & Lehmann, 2009). In addition to aromaticity, charred soil OM can have strong associations and bonding with minerals which makes them stable and prevents them from decomposition (Brodowski et al., 2005). In view of these properties, charred soil OM is a carbon stabilisation method effective for retaining carbon in the soil (Swift, 2001).

2.3.2.4 Land-use and soil organic matter preservation

Preservation of soil OM is also affected by factors other than physical and chemical protection. Through the disruption of aggregates, land cultivation enhances the release of organic molecules that become available to microbes (Elliott, 1986; Six et al., 2000). Land-use conversions have significant impact on the quantity of soil OM. The conversion of agricultural land to either pasture or forest leads to an increase in SOC stocks by 19% and 53% respectively, whereas the conversion of forest or pasture to agricultural land caused a high loss of SOC stocks, 42% and 59% respectively (Deng et al., 2016b; Guo & Gifford, 2002). In addition, land-use management affects the quantity of soil OM and properties of the soil. For example, tillage practices caused a reduction in both SOC and N pools by 26 – 55% and 7 – 34% respectively in contrast to no tillage (Mishra et al., 2010). Rahman et al. (2008) observed high soil OM under no tillage compared to that of conventional tillage. They stated that management strategies altered the basic properties (bulk density, pH, structure of microbial community) of soil following 41 years of no-tillage.

2.3.3 Factors affecting soil organic matter decomposition

2.3.3.1 Vegetation type and litter/substrate quality

The quantity and quality of fresh soil OM that enters the soil has a strong influence on the rate of soil OM decomposition. The composition, type of plants, and age of the vegetation influences the rate of decomposition (Guo et al., 2016; Hervé et al., 2019; Jobbágy & Jackson, 2000). The rate of decomposition increases with organic materials having a low C:N ratio, in contrast to a large C:N ratio (Bot & Benites, 2005). The quality of litter is defined by its structure and chemical characteristics. Generally, plants that grow faster exhibit a high rate of decomposition since morphological and chemical properties that control NPP also control the decomposition rate (De Deyn et al., 2008; Hobbie, 1992). Usually, nutrient-rich leaves decompose faster due to their richness in labile compounds like proteins and a smaller concentration of more complex macromolecules (Reich et al., 1997). In a forest ecosystem, the different litter types produce distinct kinds of litter quality with differing rates of decomposition. Mostly, decomposition is much slower in woody material than in fine litter (Chapin III et al., 2011). The progressive decay of the litter reduces the rate of decomposition as all labile compounds tend to decompose first leaving behind more complex macromolecules (Currie et al., 2010). Organic matter regulates the quality of the substrate through five

interconnected factors: i) the proportion of specific molecules as part of the whole soil OM, ii) the types of chemical bonds, iii) the structural symmetry, iv) the toxicity of specific molecules, and v) the concentration of nutrients in the soil OM (Chapin III et al., 2011; MacLean & Wein, 1978).

2.3.3.2 Soil texture and aeration

Decomposition is mostly controlled by soil aerobic microorganisms, which need oxygen as an electron acceptor. Loose structured and well-drained soils allow enough air into the soil enhancing the rate of decomposition of soil OM. In compacted soils, clayish soils, and poorly-drained soils, air is constrained from penetrating into the soil, hence reducing the rate of soil OM decay (Hervé et al., 2019). Under these poorly aerated conditions, where weaker electron acceptors are used by anaerobic microbes, soil OM tends to decompose at a slower rate and might accumulate. In any case soil aeration is enhanced when the soil is disturbed, because this disrupts soil aggregates making O_2 accessible to microbial communities (Haynes, 1986; West & Post, 2002).

Soil texture greatly affects the aeration of the soil and, consequently, the rate of decomposition. This partly explains why the content of soil OM in fine-textured soils has been found to be approximately four times more than coarse-textured soils under similar climatic and drainage conditions (Power & Prasad, 1997). Conversely, Ding et al (2014) reported that the decay of SOC in fine-textured soils is more responsive to warming compared to coarse-textured soils. Fine textured soils are more physically-protected due to the size and stability of their aggregates (Hassink et al., 1997). In addition, fine textured soils, like clay fractions, are well decayed microbial products and also form organo-mineral complexes making them more resistant to decomposition, while their formation in coarse textured soils is less favourable (Jindaluang et al., 2013).

2.3.3.3 Soil type

Soil type is an important factor that affects the rate of decomposition. Salinity, toxicity and extreme soil pH values affect biomass production and soil OM decomposition. Soils that are strongly acidic or alkaline provide poor conditions for the growth of microorganisms resulting in the decline of soil OM decomposition (Macías & Camps-Arbestain, 2020). In addition, under such conditions, especially under those that are highly alkaline, plant growth is also strongly impaired and so the input of plant detritus decreases (Jungkunst et al., 2012). The type of clay in the soil has significant effect on soil OM decomposition because each clay type exhibits peculiar features. A 2:1 clay mineral such as montmorillonite with an interlayer lattice structure has a large surface area that improves water retention, CEC, aggregate formation and keeps microbial metabolites from decomposers. Whereas a 1:1 clay like kaolinite has low water retention capacity and weakly protects C metabolite from the process of decomposition (Fissore et al., 2016). Additionally, the presence of highly reactive Al and Fe such as in allophane and ferrihydrite, respectively, reduces the rate of decomposition of organic ligands attached to them (Miltner & Zech, 1998).

2.3.3.4 Microorganisms

The breakdown of soil OM requires enzymes that are produced by microbes. The type and abundance of enzymes is largely dependent on the diversity and amount of the soil microbial community (Kaiser et al., 2010; Strickland et al., 2009). Soil microorganisms are more effective when they are in their natural environment because they have adapted to the conditions, than when there is a change in the environment. Ayres et al. (2009) reported that there was a 10% rise in litter decomposition when the breakdown occurred in the same soils where the litter was generated, in contrast to soils from a different environment. The composition and abundance of microbes is mediated by environmental factors such as temperature, moisture, availability of oxygen, and soil pH (Eilers et al., 2012). Many studies have shown a strong positive correlation between both bacteria abundance and increase in soil pH (Hartman et al., 2008; Jenkins et al., 2009; Rousk et al., 2010). Under acidic conditions, fungi tend to have a more important role than bacteria on soil OM decomposition. Although, a change in these factors may favour certain groups of microbes, their functions may be different hence affecting enzymatic activities, microbial biomass, and rate of soil OM decomposition (Talbot et al., 2013; Waldrop & Firestone, 2006). Abundance of soil OM decreases when

moving down the soil profile, affecting microbial community composition and biomass (Eilers et al., 2012).

2.3.3.5 Climate

Climatic conditions, especially temperature and precipitation, are the main components controlling soil OM abundance and storage on both global and regional scales (Wiesmeier et al., 2019). Generally, activities within the soil that are mediated by microorganisms are greater under tropical climates than in temperate soils. It is predicted that there will be an adjustment in the amount of SOC due to climatic warming. This is because processes that determine SOC balance, net plant primary productivity, and soil OM decomposition are controlled by environmental conditions (Liski et al., 1999). At present, the total net primary productivity worldwide is estimated to exceed heterotrophic (litter and soil) respiration (Bolin et al., 2000). Climate change affects the stock of soil OM by changing the growth of plants (thus changing the amount of plant debris that enters the soil) and modifying the rate of decomposition of these inputs (Jenkinson et al., 1991). Many studies have shown that temperature is a dominant factor influencing the breakdown of plant residues (Kirschbaum, 1995; McCauley et al., 2009).

The quantity of soil OM in the soil increases with an increase in rainfall. Post et al. (1982) performed a broad analysis of soil C stocks in different soils to determine the correlation between climate and SOC pools. This analysis was followed by a similar one to determine the amount of N stored in soils (Post et al., 1985). The analyses revealed that the quantity of C and N in the soil has a positive correlation with precipitation and are negatively correlated with temperature at every amount of precipitation. At high moisture content, there is an increase in plant biomass, producing greater plant residues and associated soil OM (Bot & Benites, 2005). The activities of soil microbes are higher when soil moisture is optimum, usually 60% of field capacity (Linn & Doran, 1984). The rate of soil OM decomposition reduces when moisture content falls below 30% - 50% of field capacity, because of reduction in substrate for microbes, and plant growth also falls. Also, at very high moisture content (>100% - 150% of field capacity), the rate of decay reduces due to oxygen restriction from pore spaces by the high amount of water (Haynes, 1986). Diffusion of O_2 in water is 10,000 times smaller than in air.

2.4 Modelling approaches to soil organic matter decomposition

Due to the significance of soil OM decomposition to ecosystem functioning and climate change, several models have been developed to describe its dynamics. Since the 1930s, more than 250 different models of soil OM decomposition have been proposed, with the majority of them sharing similar mathematical frameworks (Manzoni & Porporato, 2009). The approaches for modelling soil OM evolve continually. The modelling of the decomposition of soil organic matter must ideally be based on the mechanistic comprehension of soil dynamics. It should employ soil OM pools based on measured data and be effectual across more than one scale. However, no single model has fit all these criteria (Campbell & Paustian, 2015).

The models for conceptualizing organic matter decomposition are categorized into theory-driven and data-driven models. Q-model is a prime example of theory driven models. In the Q-model, decomposition is portrayed as carbon atoms having a quality feature that changes over time. The model uses the activation energy concept and links the carbon quality to temperature (viewed as intrinsic property) (Wetterstedt, 2010). Usually, the result is a mathematical formula that can be transformed into a computer model using software packages like SOILR in R programming software (Sierra, 2012). In the data-driven approach, the model is directly fed with data or changed into correlations and simple functions used as frameworks. Linking of these building blocks needs abstract perceptiveness. An example of a data-driven model is the CENTURY model (Parton et al., 1987).

Most studies that have been carried out to quantify the kinetics of soil OM decomposition have distinguished C pools that have different mean residence times (MRT) in the soil. The MRT is the inverse of the rate of decomposition and it reflects the combination of the underlying reactivity of the pool and the ambient constraints. Specifically, CENTURY and ROTH-C (Jenkinson, 1990; Parton et al., 1987) models separate SOC into conceptual pools, including decomposable plant residues close to the surface of the soil, and three pools containing C in the mineral soil, with MRT ranging from years to millennia. The breakdown of plant detritus in the soil surface depends on well-substantiated functions on climate and indices of substrate's ability to decompose (Melillo et al., 1982). The three C pools, from the most labile, to resistant to decomposition, are represented as 'fast', 'slow; and 'passive' in CENTURY but in ROTH-C, they are denoted as 'microbial biomass', 'humified organic matter' and 'inert' respectively (Six et al., 2002a; Trumbore et al., 1996). The CENTURY and ROTH-C models are still in use; they are helpful since they take into consideration the dynamics of soil OM and view soil OM as having carbon pools which decompose at distinct time periods (Blankinship et al.,

2018). Another useful model which takes into accounts microbial interactions in soil OM decomposition is the SOMic model (Woolf & Lehmann, 2019).

It has been agreed that, using conceptual pools in soil C models to predict changes in SOC reserves is better than treating soil as a single uniform pool, though the measurement of the MRTs and sizes of these pools may be inaccurate (Jones et al., 2005; Powlson, 2005; Trumbore, 2000). A significant proportion of the soil OM is contained within the passive pool that decomposes slowly. Most of the models of soil C dynamics assume that the decomposition of all soil OM is almost equally responsive to temperature. However, the rate of decomposition may be reduced, especially in the long-term after all labile C has been decomposed leaving recalcitrant C. This could be attributed to restricted access of enzymes to their molecules due to ambient constraints (Chapin III et al., 2011; Davidson & Janssens, 2006).

2.5 Temperature sensitivity to soil organic matter decomposition

The temperature sensitivity of biological systems is often represented in terms of Q_{10} (Kirschbaum, 1995), which is a measure of the rate of change of a biological or chemical system as a consequence of increasing the temperature by 10 °C. The Arrhenius function has been employed (e.g., Ellert and Bettany (1992)) to provide a better theoretical framework for Q_{10}. The Arrhenius function is a formula for determining the temperature dependence of the rates of chemical reactions. It was developed based on the equation proposed by van't Hoff, who stated that a change in equilibrium constant in chemical reactions is attributed to a change in temperature. Arrhenius realized that chemical reactions often require activation energy (E_a) to proceed. Hence, the equation: $k = Ae^{-E_a/RT}$ where k is the constant of reaction rate; E_a is the required activation energy; R is the gas constant; T is the temperature (in kelvin) and A is the exponential factor. This function forecasts that the Q_{10} of chemical reactions will decrease with increasing temperature (Davidson & Janssens, 2006).

Many environmental constraints affect the intrinsic temperature sensitivity of soil OM decomposition, reducing the 'apparent' temperature sensitivity of it. These constraints may also be responsive to climate (Davidson & Janssens, 2006). Conant et al. (2011) argued that attention should be paid to investigating how temperature influences the various factors regulating the decomposability of soil OM. This is because according to the kinetic theory, the biological and chemical processes that constrain soil OM decomposition are affected by temperature. Consequently, soil OM decomposition becomes accelerated with an ephemeral

temperature increase, due to the associated steep rise in enzyme-catalysed reactions' rates, particularly in the low-temperature range (Allison et al., 2010; Kirschbaum, 2006).

According to Blagodatskaya et al. (2016), soil microbes adapt to temperature (thermal adaptation) through these three proposed mechanisms:

(1) a shift in substrate affinity (K_m) of enzymes (Bradford, 2013), which may reflect a change in the microbial community structure (Wieder et al., 2013),

(2) a decrease in soil microbial biomass and enzymes expression at higher temperatures (Wallenstein et al., 2010), and

(3) changes in the amount and properties of substrate, affecting the rates of enzyme-mediated processes (Hartley et al., 2007).

Temperature, therefore, controls biogeochemical processes by regulating microbial metabolism (Razavi et al., 2016).

The availability of decomposable substrate is reduced by inaccessibility due to small pore neck and binding to reactive surfaces (Six et al., 2002a). Climate and soil management affect the formation of aggregates that physically protect soil OM. However, while these processes are not directly related to temperature (Davidson & Janssens, 2006), the effect of temperature on the protection of soil aggregates has not been studied in detail (Conant et al., 2011). Plante et al. (2009) observed that the temperature sensitivity of soil OM released after crushing of aggregates was not different from that of non-occluded soil. Another study done by Qin et al. (2019) on Cambisols, established that the topsoil is more responsive to high temperatures than the subsoil. The reason for this is soil OM protection is higher in the subsoil, due to the small OM/mineral ratio at depth, where there is a larger fraction of organo-mineral complexes (Blagodatskaya et al., 2014; Dungait et al., 2012). This soil OM at depth is more microbially-derived. The activity of soil microbes strongly relies on temperature, provided all the other factors influencing decomposition are not restricted (Zimmermann et al., 2012).

Studies have shown that the CO_2 efflux is dependent on the quality and quantity of available substrate, temperature, and other factors that influence the activities of decomposers. In systems where litter input does not change throughout the year, substrate depletion occurs faster in warmer summer months. But its accumulation occurs rapidly in cooler winter months, when there is less decomposer activity (Kirschbaum, 2006). Adsorption and desorption processes of the substrate are dependent on temperature (Davidson & Janssens, 2006).

According to Le Chatelier's principle, for exothermic reactions, an increase in temperature decreases the equilibrium constant (i.e. the reaction shifts toward the reactants), whilst in endothermic reactions an increase in temperature shifts the reaction toward the products. Thus a rise in temperature should increase desorption over adsorption, implying that substrate availability (the non-sorbed proportion) increases at warmer temperatures (Conant et al., 2011).

There is a lot of disagreement in the literature about temperature sensitivity of labile and preserved soil OM. Both labile and preserved soil OM have been reported to be temperature sensitive (Fang et al., 2005). Yet some authors have reported that the rate of decomposition of the preserved soil OM is more sensitive to temperature compared to the labile substrate (Conant et al., 2008; Karhu et al., 2010; Lefèvre et al., 2014; Plante et al., 2010). In contrast, some researchers have also concluded that preserved soil OM is temperature insensitive or tolerant (Giardina & Ryan, 2000; Melillo et al., 2002) and reported that labile soil OM is more temperature sensitive than preserved soil OM (Knorr et al., 2005). Despite these arguments, it is clear that climatic warming has the potential to change the chemical properties of the preserved SOC, making it accessible to microbes and consequently decomposing at a faster rate than it has been previously thought (Frey et al., 2013; Sanderman et al., 2016).

The rate of soil OM decomposition decreases with increasing altitude due to a decline in temperature and an increase in precipitation, which may favour waterlogging conditions (Tashi et al., 2016). Though the work of Tan and Wang (2016) gave a contradictory conclusion to this correlation, the general principle is that rate of decomposition declines with elevation. This is due to a reduction in temperature which alters the activities of the soil microbes, soil type and vegetation (Sierra & Causeret, 2018).

There have been divergent views regarding the decline in soil OM decomposition in volcanic soils as altitude increases. Some authors attribute it to physical protection by allophanic minerals and decline in microbial activity (Li et al., 2016; Naafs et al., 2004), others attribute it to the increase in preserved carbon from both vegetation and litter quality (Wang et al., 2016). Yet others have attributed the decline in soil OM decomposition in volcanic soils to low soil temperature with elevation (Dieleman et al., 2013; Lemenih & Itanna, 2004). Understanding the relationship between these factors will help to predict the future of soil OM in highland areas with climatic warming. Studies of Zimmermann and Bird (2012) and Zimmermann et al. (2009) established that the decline in soil OM decomposition in mountainous areas with elevation was due to declining temperatures. Though the other aforementioned factors

(physical protection, decline in microbial activity, vegetation and litter quality) also play a role in soil OM decomposition, however, temperature is considered as the most influential factor controlling decomposition. Hence there is the need to understand the temperature sensitivity of soil OM decomposition so that we can predict the effects of global warming on SOC stocks (Meyer et al., 2018).

3.0 Chapter 3: Materials and Methods

3.1 Study Area

The Egmont National Park has an active volcano, Mt Taranaki, (Higgins, 1996) located on the western shore of the North Island of New Zealand (Figure 3.1). In this study, the eastern flank of Mount Taranaki was sampled (see detailed location in Table 1). Mt Taranaki was selected for this study because it has contrasting temperature regimes from low to high altitude, with Mean Annual Temperature (MAT) ranging from 6.7^{o}C to 9.9^{o}C as shown in Figure 3.1. However, the parent material, precipitation, vegetation and soil formation processes of the area are similar. The soil of the temperate native forest was formed from andesitic tephra of the Burrell formation A.D 1655 (Aitken, 1978; Tonkin, 1970). The soil type is categorized as Recent soil from andesitic ash based on the New Zealand soil classification system (Hewitt, 2010), or Andosol based on the World Reference Base system (World Reference Base for Soil Resource, 2015). The Mean Annual Precipitation (MAP) of the study sites are greater than 2000 mm (Figure 3.2) (Davies & Lambert, 2015). The vegetation of Egmont National Park changes with increasing altitude due to changing climatic conditions. Above 1000 metres asl, it is dominated by *leatherleaf (Brachyglottis)* and *turpentine scrub (Dracophyllum)*. *Kamahi (Weinmannia), Hall's totara (Podocarpus)* and *rata (Metrosideros)* are most common from 500 meters to 1000 meters asl, whereas the lowland (150 metres to 500 metres) contains *Tawa (Beilschmiedia), Kahikatea (Dacrycarpus dacrydioides), Pukatea (Laurelia) and Rimu (Dacrydium)* (Davies & Lambert, 2015). The topography of the area is from gentle to steep slope. The forest is moderately drained at lower elevation (460-760 m asl) but well drained at higher elevation (760 -920 m asl) (Aitken, 1978). For the purposes of this research, the sampling sites represent identical parent material, soil moisture and vegetation cover type.

Table 1: GPS coordinates and elevations of the research sites at eastern flanks of Mt. Taranaki

Research Site	GPS Coordinates	Elevation (m asl)
Site 1	39°19'15.82"S; 174°11'18.05"E	512
Site 3	39°18'46.43"S; 174° 8'47.20"E	680
Site 5	39°18'20.46"S; 174° 7'8.83"E	880
Site 7	39°18'21.00"S; 174° 6'27.12"E	1024

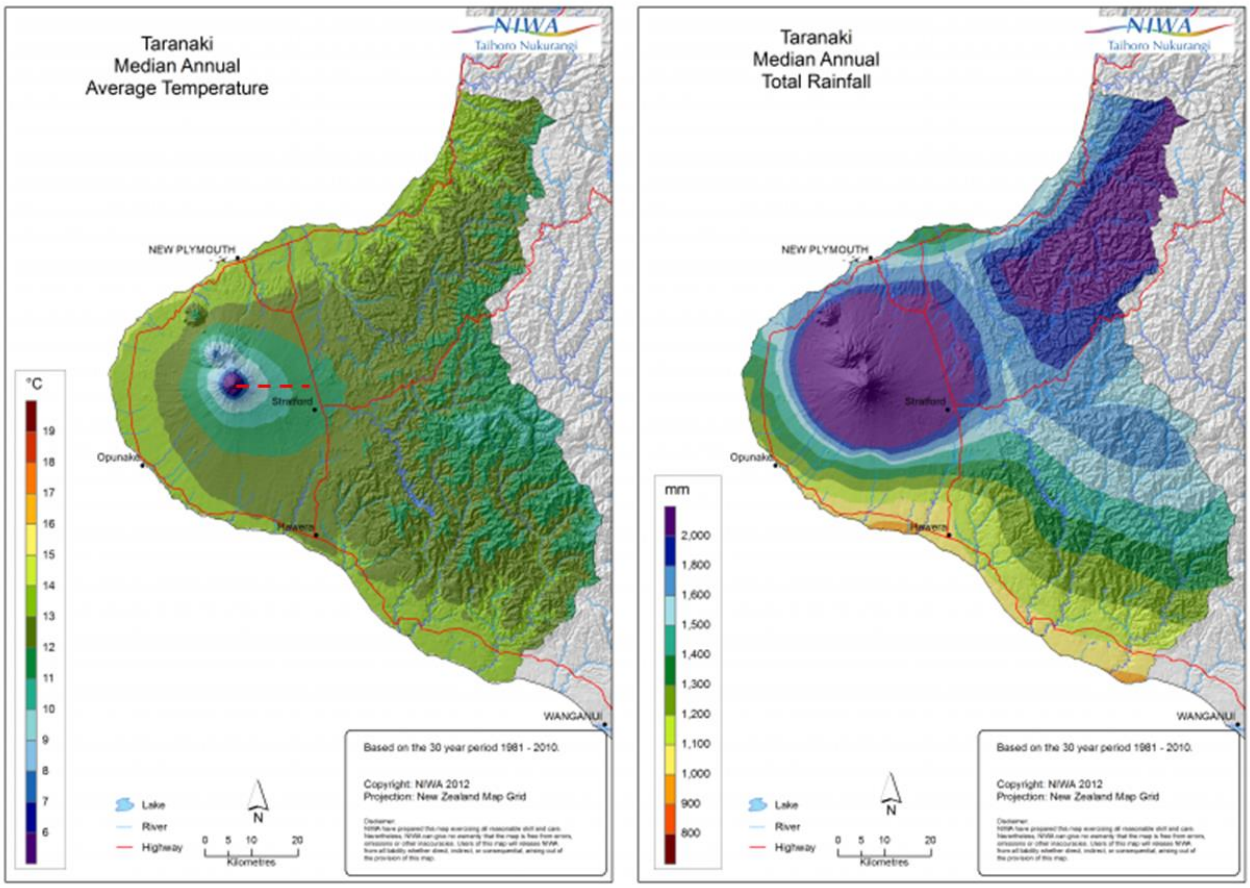

Figure 3. 1: Mean annual temperature (MAT) of sampling sites, indicated with red dot lines ranging from 6.7 to 9.9 °C (left). All transects are located within similar precipitation rate (>2000 mm), indicated by dark purple color (right). (Source: NIWA, July 2017, http://www.niwa.co.nz/climate/national-and-regional-climate-maps/taranaki). Note: Climate maps for the Taranaki Region are based on data from 1981-2010.

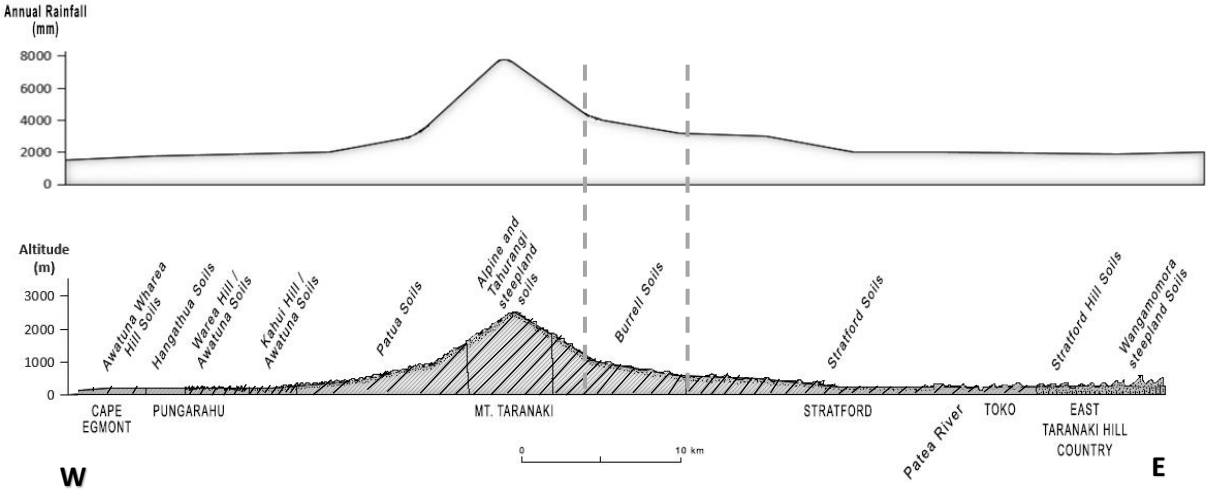

Figure 3. 2: Soil/landform and rainfall cross section from Cape Egmont to eastern Taranaki hill country (Molloy, 1988). Sampling sites were carried out in the area between the two dotted lines.

3.2 Soil Sampling

Four sites were selected at approximate 200 m vertical intervals, from 500 to 1024 m asl. Within each site, four sample locations were identified, and soils were sampled. Soils were collected using a 50 mm x 40 mm PVC pipe (cylinders) cut into a 5 cm length. The columns were inserted directly into the soil during the sampling to prevent the soils from being disturbed. The samples were taken to a depth of 40 cm at 5 cm intervals for the 25 °C temperature incubation and 10 cm interval for 5 °C, 15 °C and 35 °C temperatures. The columns with the sampled soils were stored in a chilly bin and covered with ice-cubes during transport back to the laboratory.

3.3 Sample preparations prior to incubation

Soil samples in the columns were not disturbed but incubated as taken from the field. However, due to the presence of pumice gravel at the higher elevations, soils with abundant gravel were repackaged to ensure similar conditions between replicates. For this, the four replicates of a specific layer were repacked to the same amount of soil in each soil column. Forty-seven out of the three hundred and twenty columns with soils were repackaged (Table S5.3). The base of the soil columns was sealed with plastic film (cling wrap). Before incubation, the soil samples were brought to field capacity to ensure a constant moisture content. Prior to incubation and after reaching field capacity, columns with the soils were acclimatised for 48 hours by keeping

them in the dark at room temperature (Tucker et al., 2013). Figure 3.3 summarises all the steps from soil sampling to incubation.

Figure 3. 3: Pictorial representation of the steps: A) Soil sampling to a 40cm depth at 5cm intervals B) Soils in columns ready to be irrigated to bring moisture content to field capacity C) Soils acclimatised in the dark at room temperature after field capacity and prior to incubation D) Jar with the soil column and NaOH solution in a P35 vial ready for incubation E) Samples in incubation temperature/chamber.

3.4 Soil incubation

A total number of 324 columns including four blanks were incubated. All columns contained undisturbed soil except for the repackaged ones. The blanks were four columns that had no soil and were sealed with a plastic film on both sides. The columns were put in a 500 ml jar for incubation. Twenty millilitres of 0.25 M NaOH solution was put in a P35 vial and placed beside the columns in the jar to extract CO_2 emitted from the microbial respiration. Prior to incubation, 5 ml of acidified water (0.1% HNO_3 acid) with pH of ~ 1.50 were put at the bottom of the jars to maintain a humid environment. The deionized water was acidified to reduce CO_2 solubility in water. The acidified water was replenished when needed. The jars were then incubated at 5, 15, 25, and 35 °C. Temperatures in 5, 15, and 35 °C had 65 samples each (depths: 0-5, 10-15, 20-25, and 35-40 cm), including one blank per temperature. The group incubated at temperature 25 °C had 129 samples (depths: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, 35-40 cm), including one blank. Each temperature had a sample from each of the replicates (4) taken at each sampling site (Figure 3.4). The incubation is intended to last for a period of one year. However, this work covered 190 days of incubation. The other 180 days will be continued by another student.

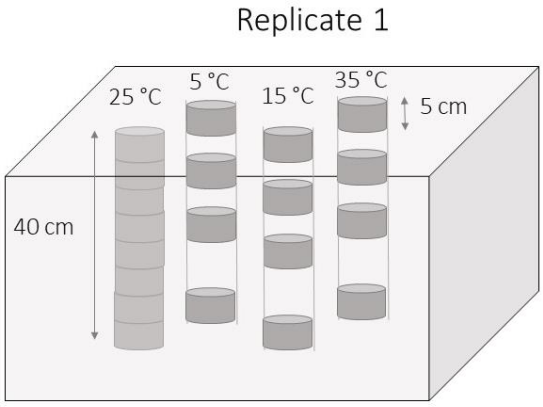

Figure 3. 4: Example of the samples taken in one of the replicates at each site. Four soil columns were sampled. For the 25 °C incubation, soil samples every 5 cm depth were taken. For the other three-temperature incubations (5, 15, and 35 °C), samples were taken at 0-5, 10-15, 20-25, and 35-40 cm depth.

3.5 Determination of CO_2 emissions

In the first week of the incubation, the P35 vial, containing 20 ml of 0.25 M NaOH solution, was removed daily. From the second week to the fourth week, the P35 vial, containing 20 ml of 0.25 M NaOH solution was removed every three days. After the fourth week, the vials with the content was removed weekly until the eighth week. Thereafter, the P35 vial, containing 20 ml of 0.25 M NaOH solution was removed fortnightly. The amount of CO_2 absorbed was determined by measuring the electrical conductivity (EC) of the NaOH solution in the P35 vials using an electrical conductivity meter HI 8733 (Hannah Instrument Limited, Bedfordshire, England) using a modified method of Woo et al. (2016). Carbon dioxide (CO_2) trapped was calculated using a linear model:

$$y = -1.9555x + 91.882 \ \ldots . Equation\ 1$$

Where y = CO_2 (ml/g); x = EC of the NaOH solution (ms/cm) with an R^2 of 0.9982

The equation 1 was determined by injecting several 500 ml jars with CO_2 of known concentration (measured with an O_2/CO_2 Integrator Analyser) through a septum lid into the jars. The jar had a 20 ml of 0.25 M NaOH solution in a P35 vial. The jars (with known CO_2 concentration and the P35 vials containing 20 ml of NaOH solution) were left in equilibrium for 24 hours to a temperature of 25 ºC. The EC of the NaOH solution in the P35 vials were measured with the electrical conductivity meter HI 8733 thereafter. A standard curve was then derived by plotting the electrical conductivity values against the CO_2 to obtain the equation 1 above.

3.6 Soil Chemical Analysis

3.6.1 Soil Sample Preparation

A subset of samples (112 samples) was analysed for their chemical composition. The soil samples were air-dried for a period of 5 – 7 days. The dried soil samples were sieved using a 2 mm mesh container and stored in plastic bags prior to analysis.

3.6.2 Determination of pH

The soil pH was determined in water using the process described by Blakemore et al. (1987). Five grams of each sample was placed into a beaker with 12.5 ml deionised water and stirred vigorously (soil: deionised water = 1:2.5). The resulting suspension was left overnight. The pH of the suspension was measured using a pH electrode.

3.6.3 Determination of Olsen P

Available phosphorus was measured following the method of Olsen (1954) and as described by Blakemore et al. (1987). For this, 1 g of air-dried soil with 20 ml of 0.5 M $NaHCO_3$ solution (pH adjusted to 8.4) was mechanically shaken for 30 minutes. The suspension was then centrifuged with speed 8000 rpm for 10 minutes. The soil extraction was then filtrated through Whatman© Grade42 filter paper. The phosphomolybdate (blue) method was used to create a blue colour that directly correlated with the phosphorus concentration. The absorbance was then measured with a spectrophotometer.

3.6.4 Organic Carbon Stocks and Organic Carbon Fractions

Approximately 1 g of fine ground soil, was further ground with a Tungsten Mill. Each sample was weighted into tin foil cups and the total soil organic carbon concentration was analysed by using Elementar, Vario MACRO, Germany (Wendt & Hauser, 2013). The pH values of the soils were < 5.8 and therefore total C of all the samples were organic. In order to estimate the short-range order constituents, materials and organo-metal complexes, the soils were extracted using 0.1 M acid ammonium oxalate (pH = 3) (Al_o, Fe_o and Si_o) following the method of Blakemore et al. (1987). The aluminium (Al) and iron (Fe) contents in organo-metal complexes were extracted using sodium pyrophosphate (Blakemore, 1981). The concentrations of Al, Fe and Si in all extractants were determined using the Microwave Plasma Atomic Emission Spectrometry (4200 MP-AES, Agilent Technologies, Singapore). The allophane content was estimated following the method of Mizota and Van Reeuwijk (1989).

The initial soil organic carbon (SOC) stocks of the soil (t C/ha) was calculated from the C content obtained from the Elementar measurement using equation 2.

$$SOC = \frac{(TC \times BD \times D \times 100)}{1000} \ldots Equation\ 2$$

Where SOC is soil organic carbon in t C/ha, TC is the total carbon in g C/kg soil, BD is the bulk density of the soil in g/cm³ and D is the soil depth in cm.

3.7 Modelling and Statistical Analysis

A three-pool exponential carbon decay model with constraints was used to analyse the data to determine the effects of temperature on the turnover rates of the pools of soil organic carbon. The rate at which the soil OM of each pool decay was calculated using rate-dependent constant modified by the temperature response function (Herath et al., 2015). The model was constrained to the initial amount of C (t C/ha) content measured at the beginning of the incubation and the C loss through respiration. The initial amount of soil C (t/ha) for the model was calculated by the addition of the SOC (t/ha) for each depth obtained from equation 2 for the specific site. The three pools (fast, intermediate and slow pools) were allocated with initial C values ensuring that their sum will be equal to the initial C stocks prior to incubation, that is

$$\sum_{i=1}^{3} C_{i(0)} = C_0 \ldots Equation\ 3.$$

The rate of CO_2 efflux was equated to the total amount of C loss from the three pools. The method of determining the temperature response function and the rate model has been described by Herath et al. (2015).

The cumulative C loss over the 190 days incubation was determined using GraphPad Prism version 7.00 software as a i) function of depth and ii) function of temperature. Statistical differences between the factors (temperature and carbon decay of each pool) were obtained by using one-way analysis of variance (ANOVA) in Minitab version 18.1 software. Tukey Least Significant Differences were considered at $P < 0.05$. To establish whether the rate of C decay was dependent on temperature, the temperature coefficient (Q_{10}) was calculated. The values for the Q_{10} was determined using the equation:

$$Q_{10} = \left(\frac{R_2}{R_1}\right) e^{\left(\frac{10}{(T_2 - T_1)}\right)} \ldots . Equation\ 4;$$

Where R_2 is the total cumulative C efflux for the 190 days at temperature T_2; R_1 is the total cumulative C efflux for the 190 days at temperature T_1; T_2 and T_1 are the incubation temperatures under comparison. T_2 is the highest temperature of the two temperatures under comparison; T_1 is the lowest temperature of the two temperatures under comparison.

4.0 Results

4.1 Soil properties

4.1.1 Soil pH, reactive Al and Fe (Al_o+½Fe_o), allophane, pyrophosphate-extractable Al (Al_p) and the ratio of Al_p and oxalated-extractable (Al_o) (Al_p/Al_o).

Soil pH tended to (i) decrease with increasing altitude (i.e., from Site 1 to Site 7, with pH at Site 1 being significantly higher at $P < 0.05$ than at Site 7 at all depths), and (ii) increase with depth – at all sites, pH at the deepest layer (35-40 cm) was significantly higher ($P < 0.05$) than at the topsoil layer (Figures 4.1a). Like the soil pH, the sum of oxalate-extractable Al and Fe (Al_o+½Fe_o) – referred to as reactive Al and Fe also tended to decrease with increasing altitude and increase with depth. At all sites considered, Al_o+½Fe_o in the deepest layer was significantly different from the topsoil layer (Figure 4.1b). The allophane content increased with depth in site 1 but was almost negligible in the rest of sites (Figure 4.1c). With few exceptions, Al_p and the Al_p/Al_o ratio increased with both altitude and depth (Figure 4.2a-b). In general, the increase with soil depth, was only significantly different ($P < 0.05$) for Al_p.

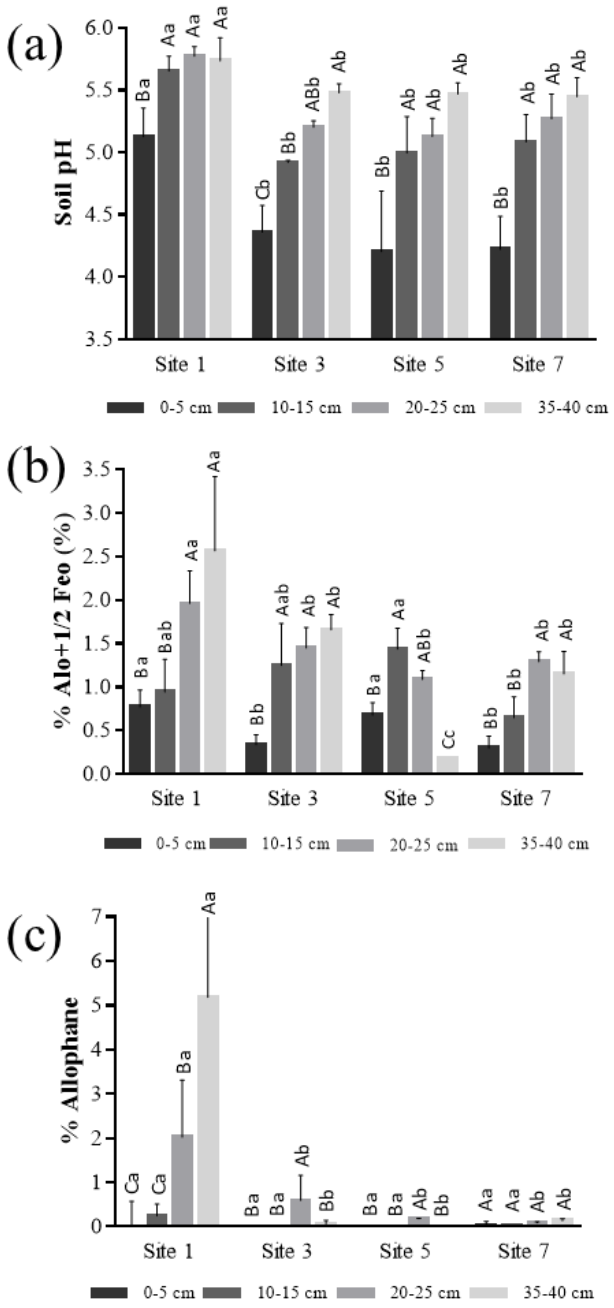

Figure 4. 1: Average and standard error of the mean of (a) pH, (b) % Alo+1/2Feo, and (c) % allophane (w/w) at each sampling site and depth. Capital letters denote comparison between the four depth at the same site, small letters represent comparison of the four different sites at the same depth. Same letters signify no significant difference between the depth of the site or the sites at the same depth.

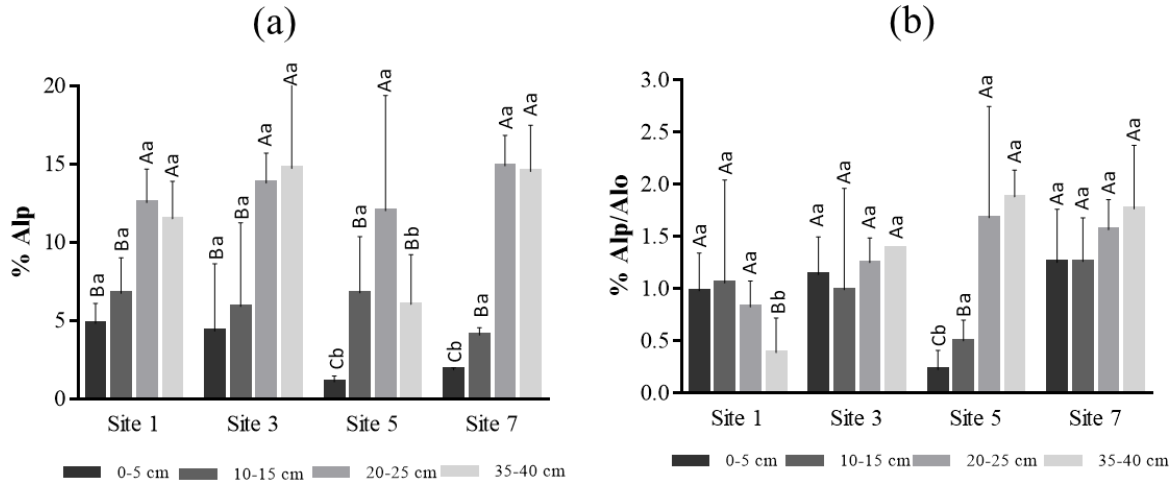

Figure 4. 2: Average and standard error of the mean of (A) concentration of Alp, and (B) Alp/Alo at each sampling site and depth. Capital letters denote comparison between the four depth at the same site, small letters represent comparison of the four different sites under the same depth. Same letters signify no significant difference between the depth of the site or the sites at the same depth.

4.1.2 Carbon content (and stocks) and C/N ratio

As expected, at all four sites, the topsoil layer had the highest C content (Figure 4.3a), and this was several folds (> 100%) that of the other layers (significant different at $P < 0.05$). There were no significant differences ($P < 0.05$) in soil C content between the rest of layers, except for sites 5 and 7, where the deepest layer had a significantly smaller value ($P < 0.05$) than the intermediate layers. There were no significant differences in C content between sites at a specific depth. The C/N ratio ranged between 12.9 and 22.8 and showed no significant differences between depths at $P < 0.05$ (Figure 4.3b). The C stocks of each soil layer followed a similar pattern to that of soil C content (Table 4.1).

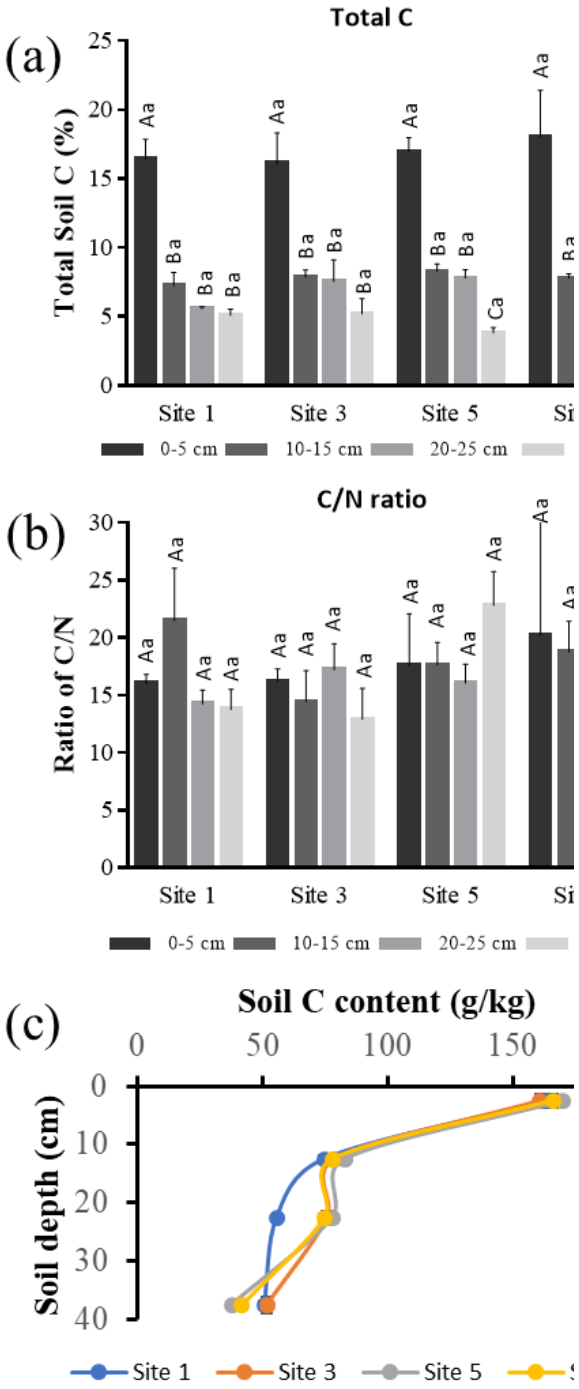

Figure 4. 3: Average and standard error of the mean of (a) Total soil C (%), (b) C/N ratio, and (c) Soil C content at depth (g/kg). Capital letters denote comparison between the four depth at the same site, small letters represent comparison of the four different sites under the same depth. Same letters signify no significant difference between the depth of the site or the sites at the same depth.

Table 4. 1: Average initial C stocks (t C/ha) and bulk density (g/cm3) with standard errors (in brackets) of the soil samples prior to incubation. Values of stocks at layers 5-10, 15-20, 25-30, and 30-35 cm depth were estimated by interpolation and the associated standard deviation calculated taking into consideration the propagation of errors. Same letters (in brackets) in the mean of the cumulative C stocks indicates no significant differences between sites.

Soil depth (cm)	Site 1		Site 3		Site 5		Site 7	
	C stocks (t/ha)	BD (g/cm^3)	C stocks (t/ha)	BD (g/cm^3)	C stocks (t/ha)	BD (g/cm^3)	C stocks (t/ha)	BD (g/cm^3)
0-5	34.3 (0.9)	0.42 (0.03)	38.6 (1.6)	0.48 (0.03)	47.9 (0.8)	0.56 (0.07)	31.3 (1.3)	0.38 (0.09)
5-10	31.1	0.47	31.3	0.48	37.4	0.52	24.8	0.42
10-15	27.8 (0.6)	0.74 (0.01)	23.9 (0.3)	0.61 (0.02)	26.8 (0.4)	0.65 (0.01)	23.1 (0.2)	0.59 (0.01)
15-20	24.5	0.66	22.4	0.50	24.7	0.65	23.5	0.63
20-25	21.2 (0.1)	0.76 (0.01)	20.9 (1.1)	0.55 (0.02)	22.6 (0.4,)	0.58 (0.02)	24.0 (0.7)	0.64 (0.01)
25-30	23.8	0.68	22.7	0.65	26.8	0.79	31.1	0.70
30-35	22.5	0.80	21.8	0.68	24.7	0.93	27.5	0.65
35-40	17.2 (0.3)	0.67 (0.02)	18.2 (0.8)	0.70 (0.03)	16.3 (0.3)	0.86 (0.04)	13.2 (0.1)	0.63 (0.02)
Cumulative $C_{0\text{-}40\ cm}$	**202.3 (B)**		**199.8 (B)**		**227.1 (A)**		**198.5 (B)**	

4.2 Cumulative carbon (C) efflux

4.2.1 Cumulative C efflux in response to soil depth

There was a rapid CO_2 loss over the initial part of the incubation. Losses decreased with depth and increased with temperature (Figures 4.4), although differences between depths were attenuated when the soils were incubated at 5°C temperature (Supplementary Figure S5.2 and supplementary Table S5.1). At all sites and at all temperatures of incubation, the top layer (0-5 cm depth) was the soil layer that had the largest cumulative C efflux, as expected. This was significantly different ($P < 0.05$) from the layers underneath. At a specific incubation temperature, soils from Sites 3 and 5, had a different cumulative C efflux at each depth considered significant at $P < 0.05$ (Supplementary Figure S5.2 and Table S5.1). This was not always the case for Sites 1 and 7, where no significant differences in cumulative C efflux were detected between 10 – 15 cm and 20 – 25 cm depth, for Site 1, and between 20 – 25 cm and 35 – 40 cm depth, for Site 7 (Figure 4.4, Figure S5.2 and Table S5.1).

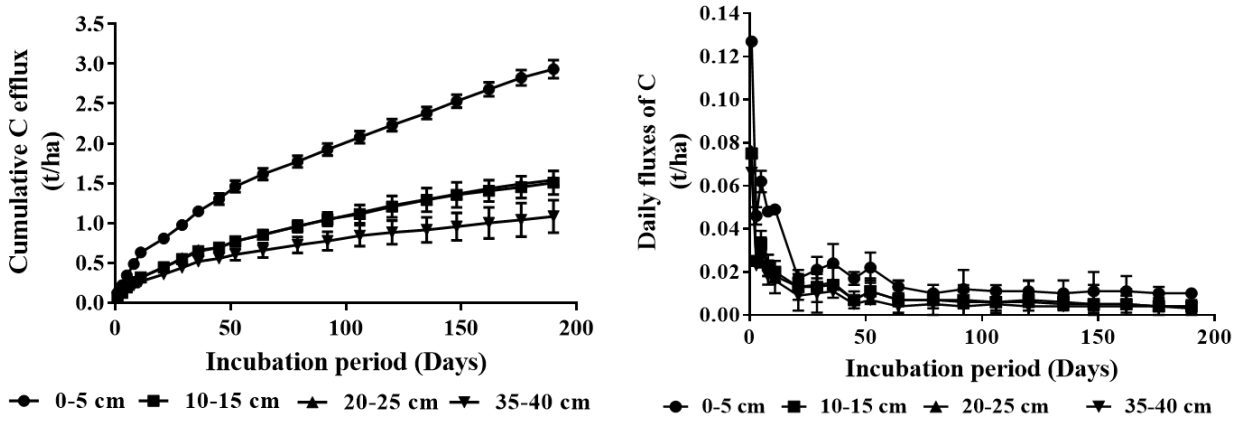

Figure 4. 4: Cumulative C efflux and daily fluxes of C (t/ha) with standard error of the mean for the different depths in Site 1 at 35°C for the 190 days of incubation.

4.2.2 Cumulative C efflux with respect to temperature

At each depth considered, the overall average cumulative C efflux was significantly different ($P < 0.05$) between incubation temperatures. The highest temperature (T35) had the largest efflux and T5 the lowest, though some exceptions were observed when looking at specific soil layers (Supplementary Figure S5.3). The influence of temperature was especially evident in the top layer where significant differences (Supplementary Table S5.1) were observed at every 10°C rise in temperature for all the sites, except for Site 7, where T35 and T25 were not significant at $P < 0.05$ (Table S5.1). At the deeper layers, cumulative C efflux was sensitive (significant at $P < 0.05$) to the same rise in temperature at some "site x depth" combinations. For instance, at 10-15 cm depth, significant differences ($P < 0.05$) were observed between T25 and T35 at Sites 1 and 5, but not at Sites 3 and 7 (Table S5.1; Figures S5.3). In these two sites (Sites 3 and 7), significant differences ($P < 0.05$) were observed between T5 and T15, as opposed to Sites 1 and 5 (Table S5.1). Similar observations were observed at 20-25 cm depth. For all sites, a 10°C rise in temperature at the deepest layer (35-40 cm depth) had no significant effect on the C efflux. This was probably influenced by the fact that at this depth changes in CO_2 evolution in response to increasing temperature were small compared with the range of randomness – but when the temperature increased to 20°C, this effect became significant.

As indicated above, the largest influence of temperature on cumulative C efflux values was observed in the topsoil (0-5 cm depth). In this layer, a temperature increase of 10 °C, caused an average increase in CO_2 efflux of 0.002% per day of the initial C content (Figure 4.5). These cumulative C efflux increments decreased down to 0.001%, in the deepest layer (Figure 4.5). The Q_{10} values consistently decreased from the topsoil layer (0-5 cm) to the deepest layer (35-40 cm), though not significantly different from each other (Figure 4.5; Table 4.2). Likewise, in general no significant differences in cumulative C efflux values between sites were observed under a specific temperature, though site 7 had the highest C efflux. For example, at 35 °C, the average cumulative C efflux values for the top layer (0-5 cm) ranged from 0.014 to 0.016 t C/ha/day, and at 5 °C from 0.004 to 0.005 t C/ha/day.

The influence of temperature was also evident when the cumulative C efflux during the 190-day incubation was calculated based on the initial C stock of each soil layer, with differences being more accentuated in the top layer (Figure 4.6). The cumulative C efflux/initial C stock was ~3 times higher at the highest temperature (T35) in comparison to the lowest temperature (T5) at all layers. Mean values of cumulative C efflux/C stock for each layer ranged from 0.3 – 1.5%, 0.2 – 0.5%, 0.1 – 0.5% and 0.1 – 0.4% for 0-5 cm, 10-15 cm, 20-25 cm and 35-40 cm

layers, with the largest values observed at 35°C and the minimum values at 5°C (Figure 4.6). Apart from the top layer, which was significantly different (at $P < 0.05$) from the other layers across all temperatures and sites, differences between the three bottom layers were not significant when the C efflux was expressed as a percentage of the initial soil C stocks (Figure 4.6). When comparing sites, significant differences (at $P < 0.05$) were only observed in the top layers, with site 5 having a generally lower cumulative C efflux/soil C compared with the rest of sites, and to a lesser extent with site 3, which had the second lower cumulative C efflux/soil C. However, the total C efflux recorded per site showed no significant differences between sites at all incubation temperatures (Supplementary Figure 5.3, Table S5.1).

The summary provided in Figure 4.7 shows that, when averaged across temperatures, it was evident that, for the topsoil, as altitude increased from Site 1 to Site 5, C efflux was smaller, but a sharp increase was observed with Site 7 (Figures 4.7c). When averaged across depths, it showed that, while the site did not have a significant effect, efflux from site 7 was always larger than for the other sites (Figure 4.7a). When averaged across sites, changes in C efflux was only significant in the top layer with increasing temperature, with no significant effect of temperature at deeper layers (Figure 4.7b)

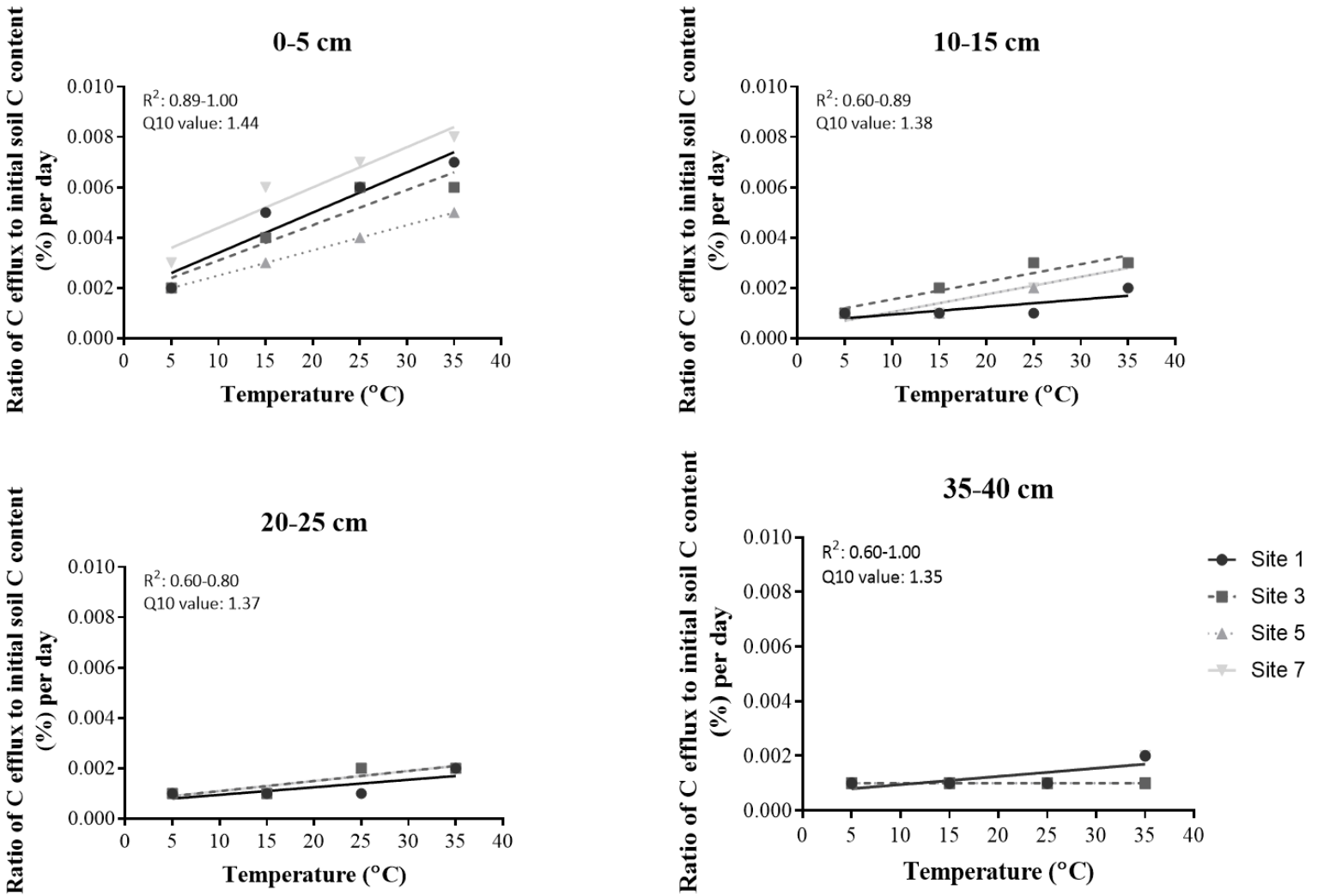

Figure 4. 5: Estimated C efflux out of the initial C content (%) per day at each depth at the different incubation temperature regimes over the length of the incubation period.

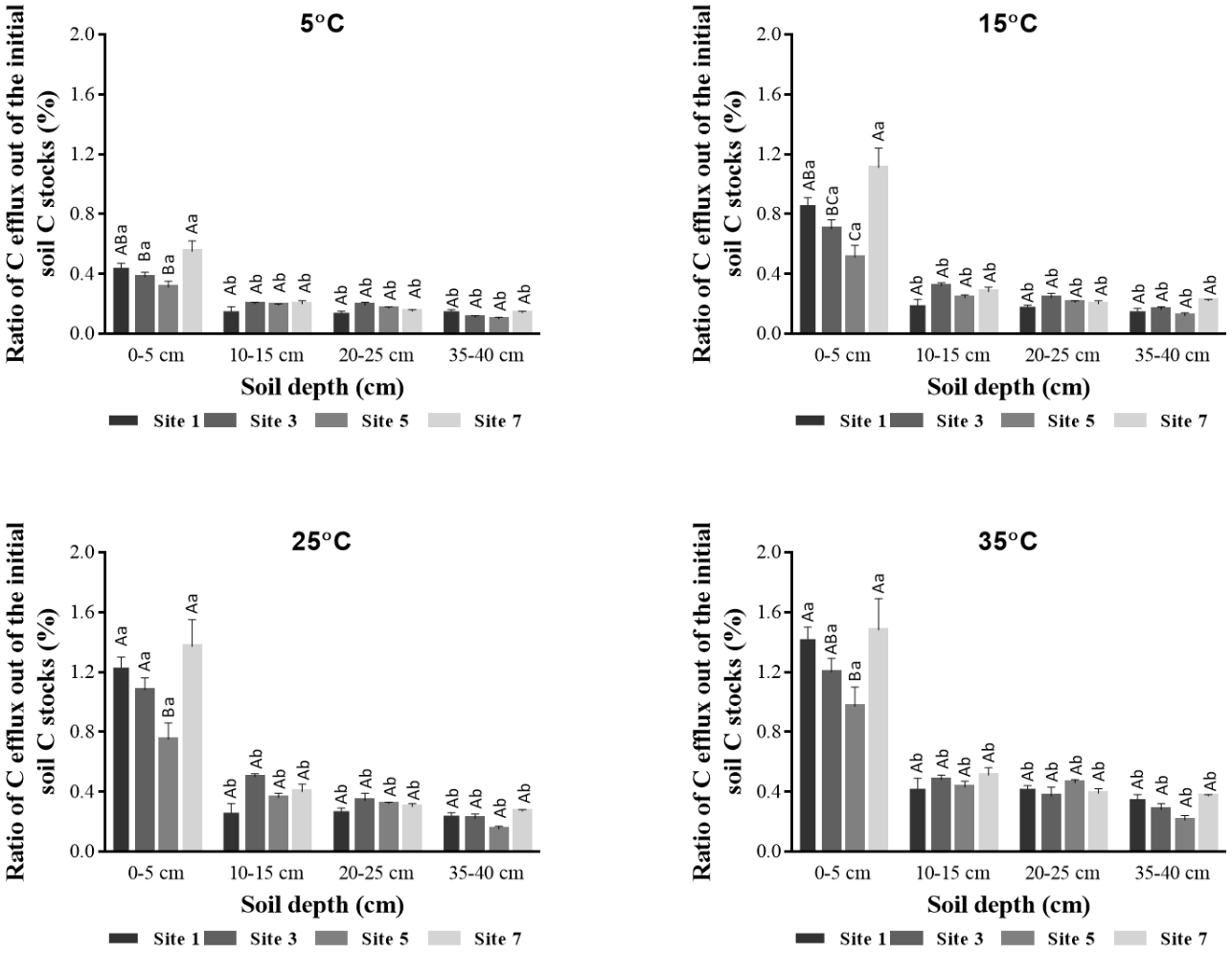

Figure 4. 6: Ratio and standard error of the mean of C efflux out of initial soil C stocks (in %) at the end of a 190-day incubation of soils from 4 sites and sampled at 4 depths at the different temperatures. Capital letters denote comparison between the four sites at the same depth (same letters mean not significantly different) whereas small letters represent comparison of the four different depths at the same site under a given temperature (same letters mean that depth was not significantly different at the corresponding site).

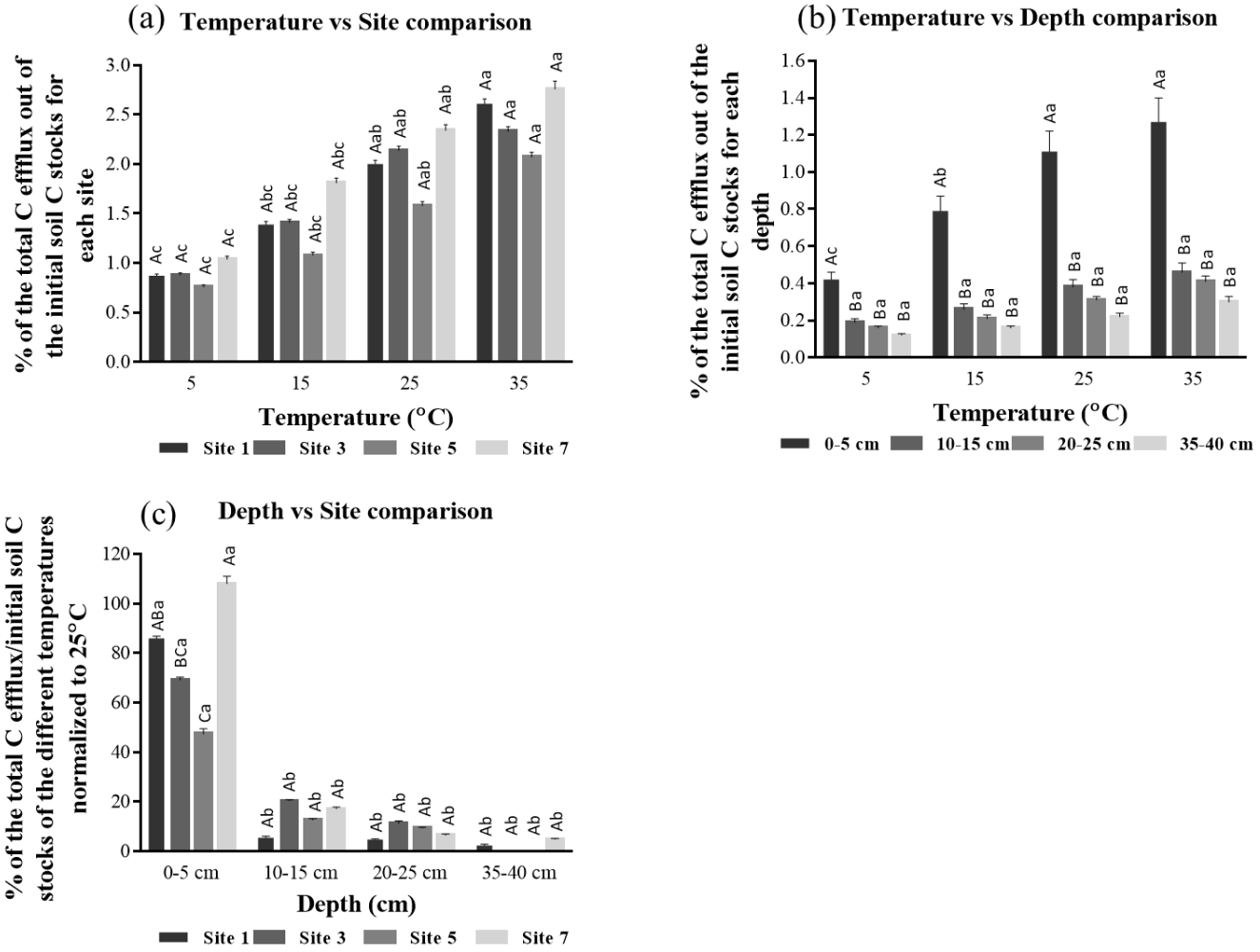

Figure 4. 7: Comparison of total C efflux/C stocks and standard error of the mean with respect to (a) Temperature and site, (b) Temperature and depth, and (c) Site and depth at the end of a 190-day incubation. Capital letters denote comparison between the four sites/depth at the same temperature/depth whereas small letters represent comparison of the four different temperatures/depths at the same site/depth. Same letters signify not significant.

Table 4. 2: Temperature coefficient (Q10) of the average cumulative C efflux (t/ha/190 days) for the four sites and depths under the four incubation temperatures interactions. Capital letters denote comparison of the temperature interactions at the same depth, small letters represent comparison between specific temperature interactions and depths at the same site.

Temperature interactions	Site 1				Site 3				Site 5				Site 7			
	0-5 cm	10-15 cm	20-25 cm	35-40 cm	0-5 cm	10-15 cm	20-25 cm	35-40 cm	0-5 cm	10-15 cm	20-25 cm	35-40 cm	0-5 cm	10-15 cm	20-25 cm	35-40 cm
T15 vs T5	1.98 Aa	1.31 Aa	1.30 Aa	1.02 Aa	1.85 Aa	1.56 Aa	1.25 Aa	1.40 Aa	1.66 Aa	1.26 Aa	1.29 Aa	1.22 Aa	1.41 Aa	1.31 Aa	1.31 Aa	1.55 Aa
T25 vs T5	1.68 Aa	1.33 Aa	1.38 Aa	1.29 Aa	1.70 Aa	1.57 Aa	1.34 Aa	1.39 Aa	1.55 Aa	1.38 Aa	1.39 Aa	1.25 Aa	1.42 Aa	1.41 Aa	1.41 Aa	1.39 Aa
T35 vs T5	1.48 Aa	1.42 Aa	1.43 Aa	1.34 Aa	1.47 Aa	1.33 Aa	1.25 Aa	1.35 Aa	1.45 Aa	1.32 Aa	1.40 Aa	1.31 Aa	1.37 Aa	1.37 Aa	1.37 Aa	1.38 Aa
T25 vs T15	1.42 Aa	1.35 Aa	1.47 Aa	1.62 Aa	1.56 Aa	1.57 Aa	1.43 Aa	1.38 Aa	1.46 Aa	1.52 Aa	1.50 Aa	1.28 Aa	1.43 Aa	1.52 Aa	1.52 Aa	1.25 Aa
T35 vs T15	1.28 Aa	1.48 Aa	1.50 Aa	1.53 Aa	1.31 Aa	1.23 Aa	1.25 Aa	1.32 Aa	1.37 Aa	1.35 Aa	1.46 Aa	1.36 Aa	1.35 Aa	1.40 Aa	1.40 Aa	1.31 Aa
T35 vs T25	1.15 Aa	1.62 Aa	1.53 Aa	1.46 Aa	1.11 Aa	0.96 Aa	1.10 Aa	1.27 Aa	1.30 Aa	1.20 Aa	1.42 Aa	1.44 Aa	1.27 Aa	1.29 Aa	1.29 Aa	1.36 Aa

4.2.3 Influence of temperature on the turnover rate of C

When pooling all the data from the four sites together, Figure 4.8 shows that the turnover rate of C of the different C pools investigated (fast, intermediate, slow), as estimated by a three-pool carbon model, was significantly influenced ($P < 0.05$) by the temperature of incubation. For the fast pool, the C turnover rate was largest (significant at $P < 0.05$) at the highest temperatures (T25 and T35) (mean values for T25 from top to the deepest layer were 11.2, 9.6, 7.1 and 5.2 t C/ha/day, respectively; and that of T35 were 12.9, 10.9, 9.6 and 7.5 t C/ha/day, respectively) and lowest (significant at $P < 0.05$) at the lowest temperatures (T5 and T15) (mean values for T5 were 1.7, 1.0, 0.8 and 0.7; and for T15, the mean values were 2.8, 1.7, 1.3 and 0.8 t C/ha, respectively) at all depths and sites (Figures 4.8 and 4.9). With few exceptions, the influence of altitude was generally not significant (Figure 4.9). At 25 °C, the turnover rate tended to be higher as altitude increased, with the highest altitude (Site 7) being significantly different ($P < 0.05$) from the lowest altitude (Site 1) at all depths, except for the 35-40 cm layer, but these differences were less evident at other temperatures of incubation (Figure 4.9). For the fast pool, the turnover rate of the top layer was generally significantly higher ($P < 0.05$) than the other layers when incubated at the highest temperatures (T25 and T35) in contrast to the lower temperatures (T15 and T5) where no significant difference was observed (Figures 4.8 and 4.9).

For the intermediate and the slow pools, a more gradual increase in turnover rate was observed as temperature of incubation increased (Figures 4.8 and Supplementary Figures S5.4 and S5.5). For the intermediate pool, mean values were 0.02 ~ 0.02 ~ 0.04 < 0.07 t C/ha (for the top layer); 0.02 ~ 0.01 < 0.03 ~ 0.05 t C/ha (for 10-15 cm layer); 0.02 ~ 0.02 < 0.03 < 0.06 t C/ha (for 20-25 cm layer); 0.02 ~ 0.02 < 0.04 < 0.06 t C/ha (for 35-40 cm layer) for T5, T15, T25, and T35, respectively, whereas for the slow pool, these were $1.2x10^{-5}$ ~ $2.2x10^{-5}$ < $4.0x10^{-5}$ ~ $5.5x10^{-5}$ t C/ha (for the top layer); $5.0x10^{-6}$ ~ $5.0x10^{-6}$ < $1.7x10^{-5}$ ~ $2.5x10^{-5}$ t C/ha (for 10-15 cm depth); $3.0x10^{-6}$ ~ $5.0x10^{-6}$ < $1.4x10^{-5}$ ~ $2.3x10^{-5}$ t C/ha (for 20-25 cm depth); $0.1x10^{-5}$ ~ $0.2x10^{-5}$ < $0.9x10^{-5}$ < $1.8x10^{-5}$ t C/ha (for 35-40 cm depth) (Figures S5.4 and S5.5). In general, the C turnover rate of the intermediate pool was approximately 1.5 times faster than the slow pool. For the intermediate pool, differences between sites were again only apparent for samples incubated at 25 °C, whereas for the slow pool, differences between sites were also apparent at other incubation temperatures. For both pools, the turnover rate in site 5 at 25 °C, tended to be slower than in the rest of sites as opposed to that in site 7, which tended to be faster (Figures S5.4 and S5.5). Differences between soil layers were specifically evident for the slow pool,

where the turnover rate of the top layer was significantly higher ($P < 0.05$) than the rest of layers – for the intermediate pool significant differences between layers were generally inexistent (Figures S5.4 and S5.5).

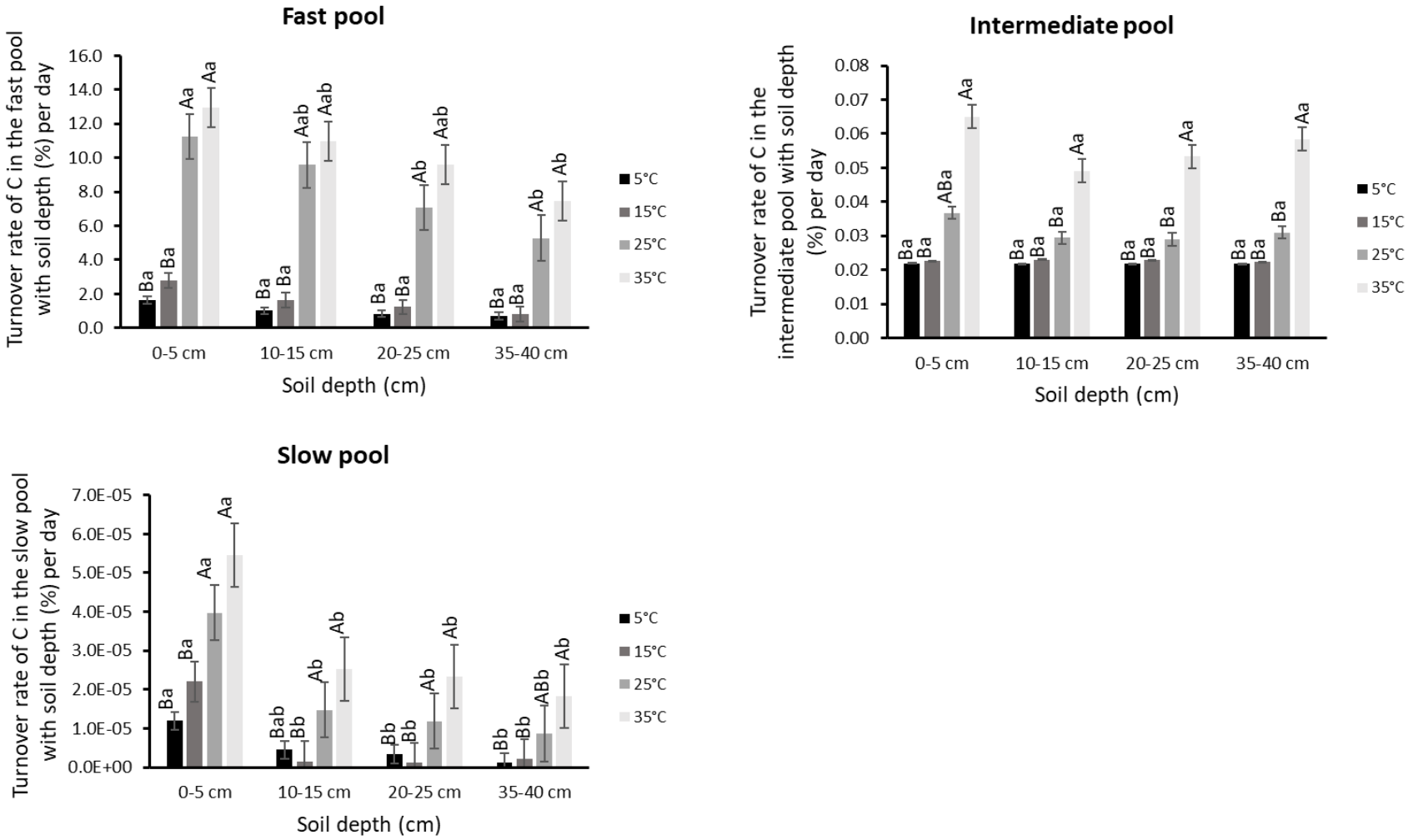

Figure 4. 8: Comparison of the influence of temperature on the turnover rate of C with soil depth in the three pools of carbon and the standard error of the mean. Capital letters denote comparison between the four temperatures at the same depth, small letters represent comparison of the four different depths at the same temperature. Same letters signify no significant difference.

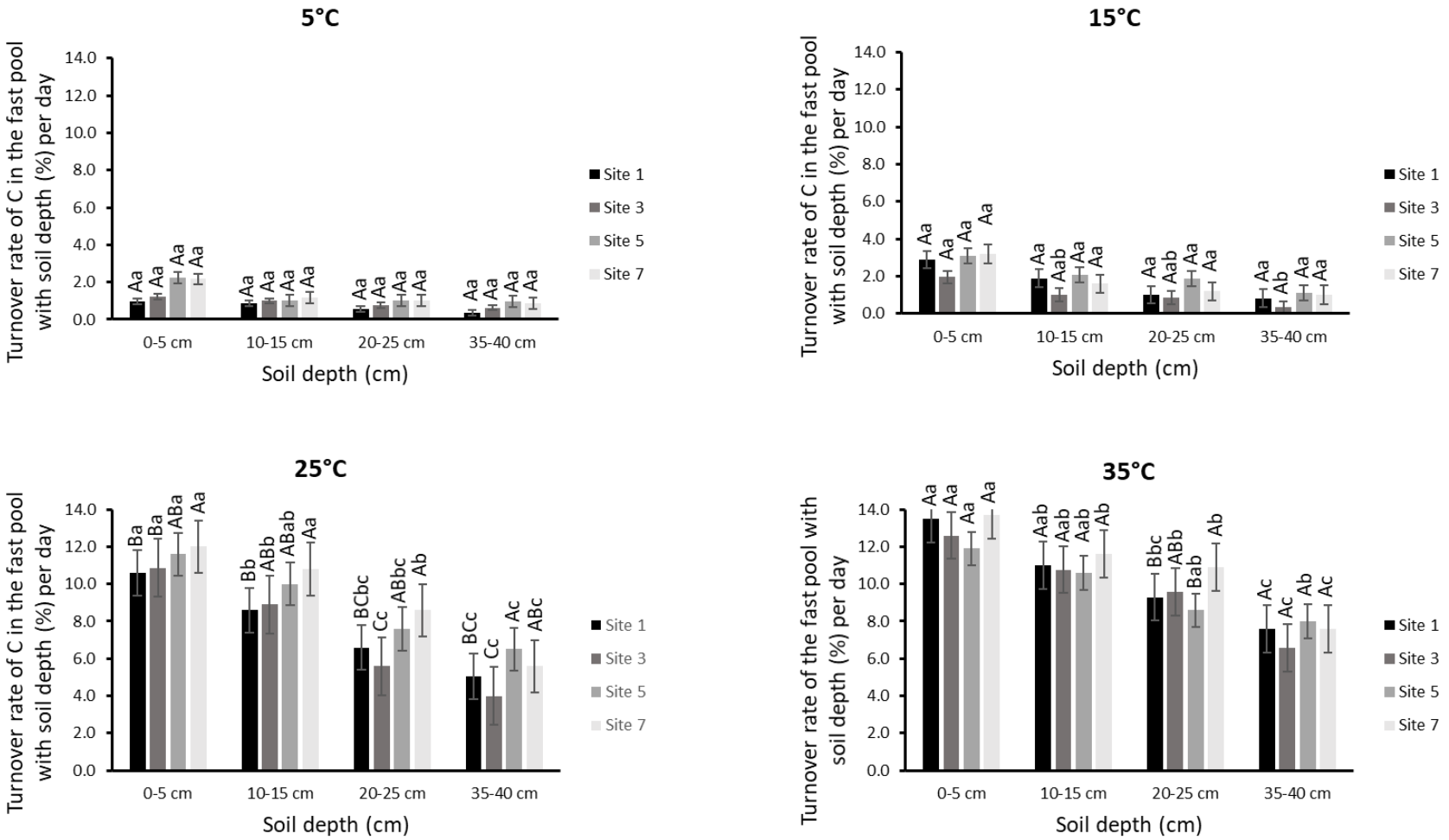

Figure 4. 9: Comparison of the influence of soil depth on the turnover rate of C in the fast pool under different temperatures from the three-pool model with constraints and standard error of the mean. Capital letters denote comparison between the four sites at the same depth (same letters mean not significantly different), small letters represent comparison of the four different depths at the same site under a given temperature (same letters mean that depth was not significantly different at the corresponding site).

4.2.4 Size/Proportions of initial C content in each pool

The proportion of initial C stocks to each pool as estimated by a three-pool C model, showed that > 99% of the soil C were stored in the slow pool. The remaining 1% was shared among the fast (0.03%) and the intermediate C (0.97%) pools. No specific pattern was observed in each pool and the response of the C distribution to a rise in temperature generally showed no trend (Figure 4.10). This suggest that the distribution of the initial C stocks to the three C pools in the model was independent of temperature. Again, with few exceptions, differences in C distribution between sites and depth was generally absent across all three pools.

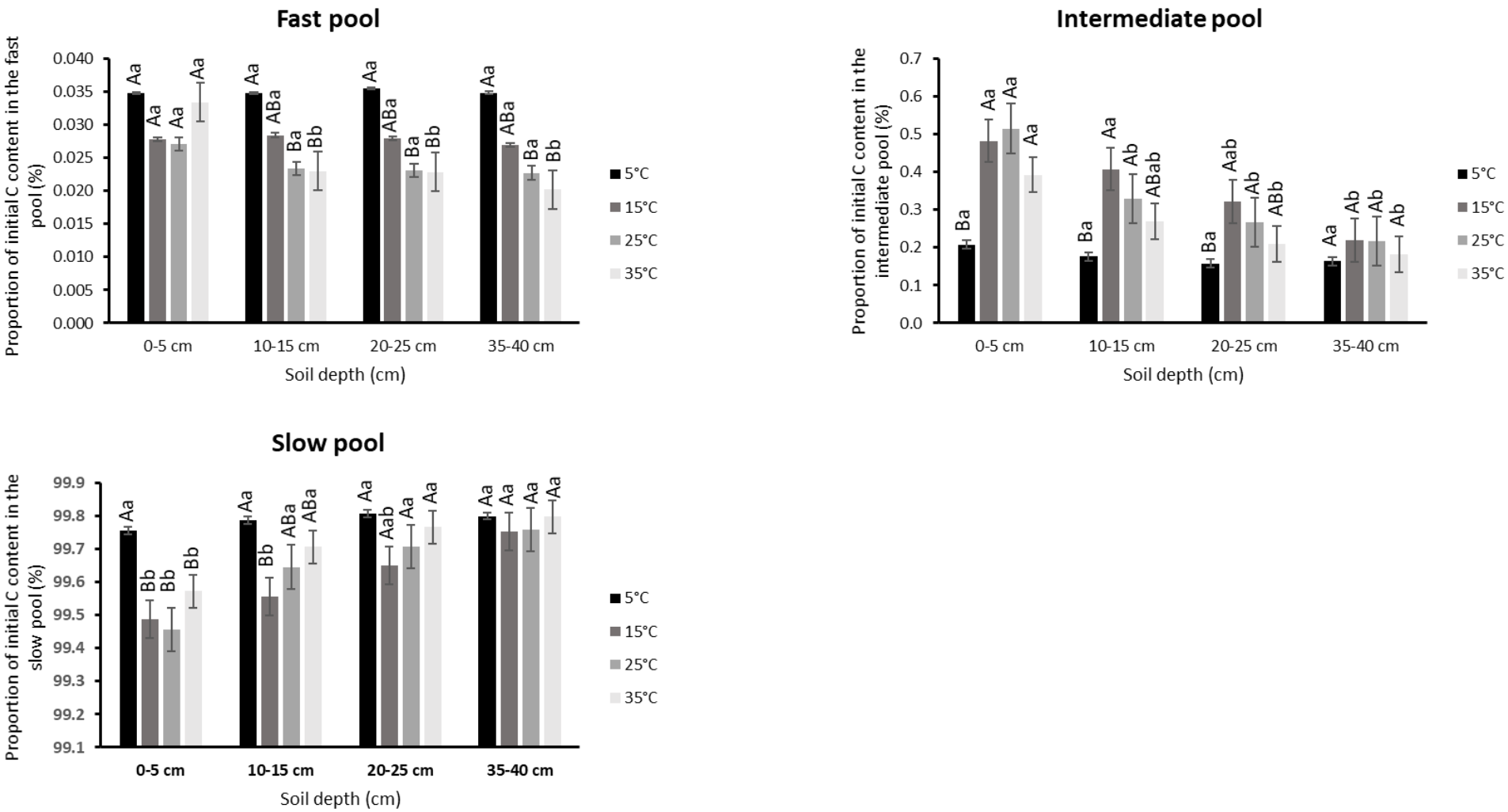

Figure 4. 10: Proportion of initial C stocks and standard error of the mean at each soil depth in the three C pools.

4.3 Principal Component Analysis

We carried out the PCA analysis including all chemical properties without (Fig. 4.11a-b) and with (Fig. 4.11c-d) the results from the incubation. When C fractions were excluded (Fig. 4.11), the four principal components accounted for 87.5% of the variability in the chemical properties, with PC1 accounting for 46.2% of the variability and PC2 accounting for 24.0% (Figure 4.11a). The factor loadings (Fig. 4.11a) showed that (i) PC1 was driven by the presence of reactive surfaces (allophane, Al_o + ½ Fe_o), with high values plotting away from a high Al_p/Al_o value; and (ii) PC2 was driven by the organic C (and total N) content, with high values plotting away from high pH values and Al_p values. The factor scores (Fig. 4.11b) showed that (i) altitude could explain the differences in reactive surfaces, with lower altitude areas plotting towards high PC1 values, consistent with higher allophane content, this being especially evident in the 35-40 cm depth; and (ii) that surface horizons were the drivers of the high organic C content and high acidity, both properties decreasing with depth. The C:N ratio was not driven by either PC1 or PC2.

When C fractions were included, the first four principal components accounted for 71.3% of the variability of SOC decomposition with PC1 and PC2 accounting for 45.8% and 14.0% respectively (Fig. 4.11c). The factor loadings (Fig. 4.11c) showed that i) PC1 was driven by organic carbon (TC) (and total N) content as well as the fast and slow C pools, which plotted away from soils with high pH and high Al_p values; ii) PC2 was driven by Al_o and Fe_o values, these plotting away from the ratio of Al_p/Al_o, and (iii) the intermediate pool was not driven by either PC1 or PC2 (Figure 4.11C). The factor scores (Fig. 4.11d) showed the correspondence between the topsoil layers (0-5 cm) with both the fast and slow C pools.

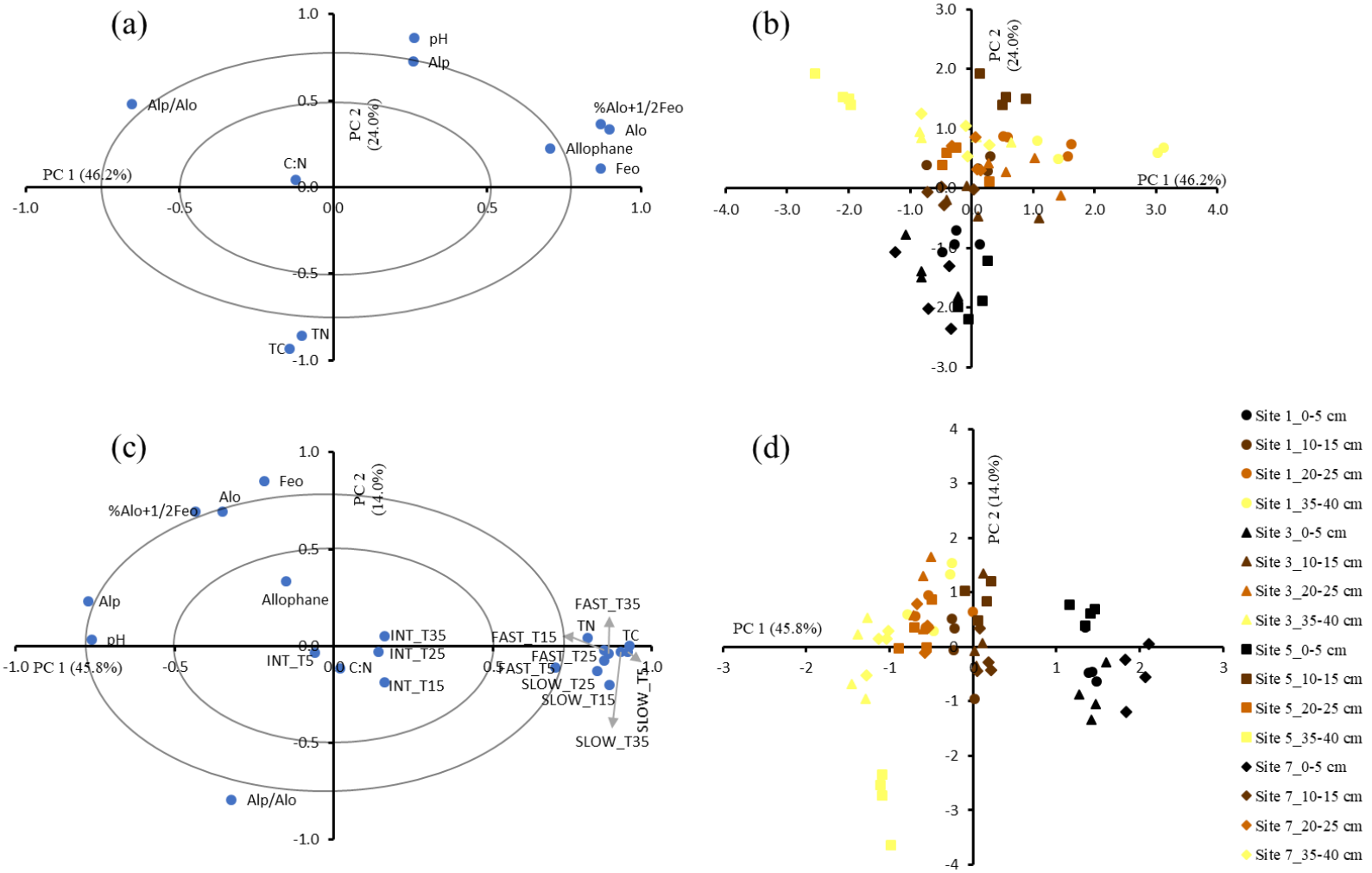

Figure 4. 11: (a) PC1-PC2 loadings of soil properties excluding C fractions for all the studied soils; (b) PC1-PC2 scores for the soil samples excluding C fractions; (c) PC1-PC2 loadings of soil properties including C fractions for the studied soils (d) PC1-PC2 scores for the soil samples including C fractions.

5.0 Discussion

5.1 Soil properties

The pH of the soil is influenced by the presence of weatherable materials, rainfall, drainage, type of vegetation, and the type and amount of soil pH-buffers (e.g., carbonates, reactive Al, cation exchange sites) (McCauley et al., 2009). In our study, the soil pH increased with depth at all sites. This was also evident in the PCA results, where the scores of the surface layers plotted away from high pH values. The increase is related to the increasing alkalinity of the system at depth, where the influence of the parent material (rich in weatherable minerals) is stronger than in the surface layers and buffers the acidity from the vegetation. The soil pH decreases from the lowest elevation (Site 1) to the highest elevation (Site 7). Several factors might have influenced this pattern. On one hand, there is a higher rainfall at the highest elevation, which causes a greater leaching of base cations compared with the site at the lowest elevation (McCauley et al., 2009). On the other hand, the tephra particle size increases closer to the summit (i.e., at higher altitude), because the settling distance of ejected tephra is strongly influenced by particle size and density, being larger closer to the source. As particle size increases, the surface area decreases and the rate of weathering also decreases (i.e., smaller release of base cations contributing to the alkalinity of the system) yet the higher rainfall closer to the summit might partly compensate for these differences.

The positive correlation of allophane with soil pH is related to an increase in hydroxyl ions as soil pH increases. This favours their interaction with Al cations, becoming stronger competitors against organic ligands for Al, as opposed to what occurs at acidic soil pH values (Dahlgren et al., 2004). The fact that formation of organo-Al compounds occurs under conditions where formation of allophane is inhibited is evident in the PCA results, where allophane values plotted away from Al_p/Al_o values. This accounted for (i) the general decrease in allophane concentrations across the different sites as altitude (and acidity) increased, and (ii) the increase in allophane content with depth at each site, as alkalinity increased (Figure 4.1). This decrease was more evident when samples were taken down to 85 cm depth (Siregar, unpublished data), as allophane content at 50 to 85 cm depth was 9.0, 5.6, 3.2 and 2.3%, at sites 1, 3, 5 and 7, respectively.

The findings were in line with those of Hunziker et al. (2019) who studied the potential of volcanic soils in carbon sequestration in southern Iceland. They observed that the soil pH increases with soil depth under each vegetation type, and there was a strong positive correlation

(r = 0.68) between soil pH and allophane concentration. Given that Al in allophane is extractable with ammonium oxalate, values of Al_o were also positively correlated with allophane content, in addition to soil pH, as also reflected in the PCA from these data. Values of pyrophosphate-extractable Al (Al_p) and the Al_p/Al_o ratio generally increased with altitude. This could be attributed to the above-mentioned decline of soil pH with altitude and the conditions being less favourable for allophane formation, as opposed to that of organo-Al complexes, this was especially evident in site 5.

5.2 Soil organic carbon cycling and temperature

5.2.1 Cumulative C efflux with soil depth and temperature

Cumulative C efflux decreased significantly with depth across all temperatures at the end of the 190 days of incubation. Specifically, there was a smaller release of CO_2 per unit of organic C with depth. This could be due to the following reasons: 1) the presence of a larger amount of undecomposed soil OM in the top layer, which is enriched in litter necromass; and 2) the smaller interaction of organic ligands with the mineral components of the soil in the top layer. In the top layer these are less chemically and physically protected, as opposed to down the profile, where also aggregation and organo-mineral interactions increase. It should be noted that, in addition to the well-known chemical interaction of reactive Al with organic ligands, Allophanic soils are characterised by a high microaggregate stability. The pores in the microaggregates prevent O_2 from diffusing into the inner part of the aggregates, further protecting soil OM from decomposition (Buurman et al., 2007).

Given that the activity of soil microbes is enhanced as temperature increases, the turnover rates of SOC are accelerated. This explains the increase in C efflux and is consistent with other studies (Billings & Ballantyne IV, 2013; Conant et al., 2008; Zhou et al., 2015). The fact that the topsoil layer had the highest cumulative C efflux with temperature could be explained by the above-stated presence of more organic detritus and the weaker organic matter protection by inorganic constituents, which makes them readily available to soil microbes (Olk & Gregorich, 2006). The findings support the study conducted on altitudinal gradients in a tropical forest gradient in Peru where the influence of rising temperature on the rate of soil respiration was assessed (Zimmermann & Bird, 2012). Unlike the topsoil layer, C efflux in the deeper layers showed a gradual increase to rising temperature which could be due to increasing mineral/chemical composition and physical protection from the microaggregates down the

profile (Zimmermann & Bird, 2012). Despite this protection in the deeper layers, a rise in temperature caused an increase in total C efflux at end of the incubation. In addition, there was an increase in C efflux per initial C content with temperature. The calculated Q10 values indicated that the C efflux in all layers was responsive to a change in temperature.

5.2.2 Temperature influence on SOC turnover rate

The C efflux in the three pools (fast, intermediate and slow C pools) responded to temperature but at different rates. The differences in C efflux in the three pools could be attributed to the differences in turnover rates of each of the pools (Hoyle & Murphy, 2006). The fast C pool was ~15 times greater than the intermediate C pool and this was ~10 times greater than the slow pool. These proportions between the three C pools did not change with depth or altitude. The short period of incubation may have accounted for the small C efflux in the slow C pool compared to the SOC in the fast C pool, which was consumed within few days at the highest temperature and approximately a week in the lowest temperature (Paul, 2016).

The high proportion of SOC allocated to the slow pool (ca. 99%) compared to the fast (0.03%) and intermediate C (0.97%) pools could be explained by the fact that Allophanic soils are able to store large amounts of soil C due to their high organo-mineral complexes. The high allocation of C in the slow pool may have contributed to the generally low C efflux observed at the end of the 190 days incubation.

6.0 Conclusions

Our study has provided the following evidences:

i) Altitude did not have an influence on the relative (Total C efflux/Initial C content of the soil) C efflux.

ii) Microbial activity, and thus soil OM decomposition, was enhanced with temperature, even at the deepest layer where there was more chemical protection and microaggregate stability.

iii) Despite the topsoil layer having the highest rate of C efflux, all the layers were responsive to a rise in temperature as no significant difference was observed between the Q10 values of all the layers.

iv) Likewise, all the sites/altitude responded equally to a change in temperature because no difference generally occurred in C efflux between sites at a specific depth. This observation was also supported by the calculated Q10 values.

v) The C pools considered (fast, slow and intermediate C) did not differ in their relative change with temperature. However, the turnover rate of the fast C pool was higher compared to the intermediate and the slow C pools.

The findings from this study have provided further understanding on how accelerating temperature affects organo-mineral complexes and the cycling of soil organic carbon, specifically, on the rates at which this occurs. Yet given that the rate of C loss in the deeper layers was very small, more work with a long incubation period should be conducted to better appreciate the influence of temperature to C cycling.

7.0 Supplementary information

Table S5. 1: Average of the cumulative C efflux (t/ha/190 days) for the four sites and the four incubation temperatures. Capital letters denote comparison of the four depths at the same site under a given temperature whereas small letters represent comparison between different temperatures at the same site and depth.

Depth	Cumulative C efflux (t/ha)															
	Site 1				Site 3				Site 5				Site 7			
	5°C	15°C	25°C	35°C	5°C	15°C	25°C	35°C	5°C	15°C	25°C	35°C	5°C	15°C	25°C	35°C
0-5 cm	0.91 Ad	1.80 Ac	2.57 Ab	2.97 Aa	0.90 Ad	1.67 Ac	2.59 Ab	2.88 Aa	0.87 Ad	1.44 Ac	2.10 Ab	2.72 Aa	1.03 Ac	2.09 Ab	2.58 Aa	2.80 Aa
10-15 cm	0.55 Bc	0.72 Bbc	0.97 Bb	1.57 Ba	0.62 Bc	0.97 Bb	1.52 Ba	1.46 Ba	0.61 ABc	0.77 Bc	1.17 Bb	1.54 Ba	0.59 Bc	0.83 Bbc	1.19 Bab	1.52 Ba
20-25 cm	0.53 Bc	0.70 Bc	1.03 Bb	1.58 Ba	0.52 Bb	0.65 Cb	0.93 Ca	1.01 Ca	0.47 Bc	0.62 Bc	0.93 Bb	1.32 Ba	0.49 Bc	0.63 Bbc	0.97 Bab	1.25 Ba
35-40 cm	0.49 Bc	0.50 Bc	0.81 Bb	1.18 Ca	0.40 Bc	0.56 Cbc	0.77 Cab	0.98 Ca	0.41 Bb	0.50 Bb	0.64 Bab	0.92 Ca	0.44 Bc	0.68 Bbc	0.85 Bab	1.16 Ba

Table S5. 2: Temperature coefficient (Q10) of the average cumulative C efflux (t/ha/190 days) for the four sites and depths under the four incubation temperatures interactions. Capital letters denote comparison of the temperature interactions at the same depth whereas small letters represent comparison between specific temperature interactions and depths at the same site.

Temperature interactions	Site 1				Site 3				Site 5				Site 7			
	0-5 cm	10-15 cm	20-25 cm	35-40 cm	0-5 cm	10-15 cm	20-25 cm	35-40 cm	0-5 cm	10-15 cm	20-25 cm	35-40 cm	0-5 cm	10-15 cm	20-25 cm	35-40 cm
T15 vs T5	1.98 Aa	1.31 Aa	1.30 Aa	1.02 Aa	1.85 Aa	1.56 Aa	1.25 Aa	1.40 Aa	1.66 Aa	1.26 Aa	1.29 Aa	1.22 Aa	1.41 Aa	1.31 Aa	1.31 Aa	1.55 Aa
T25 vs T5	1.68 Aa	1.33 Aa	1.38 Aa	1.29 Aa	1.70 Aa	1.57 Aa	1.34 Aa	1.39 Aa	1.55 Aa	1.38 Aa	1.39 Aa	1.25 Aa	1.42 Aa	1.41 Aa	1.41 Aa	1.39 Aa
T35 vs T5	1.48 Aa	1.42 Aa	1.43 Aa	1.34 Aa	1.47 Aa	1.33 Aa	1.25 Aa	1.35 Aa	1.45 Aa	1.32 Aa	1.40 Aa	1.31 Aa	1.37 Aa	1.37 Aa	1.37 Aa	1.38 Aa
T25 vs T15	1.42 Aa	1.35 Aa	1.47 Aa	1.62 Aa	1.56 Aa	1.57 Aa	1.43 Aa	1.38 Aa	1.46 Aa	1.52 Aa	1.50 Aa	1.28 Aa	1.43 Aa	1.52 Aa	1.52 Aa	1.25 Aa
T35 vs T15	1.28 Aa	1.48 Aa	1.50 Aa	1.53 Aa	1.31 Aa	1.23 Aa	1.25 Aa	1.32 Aa	1.37 Aa	1.35 Aa	1.46 Aa	1.36 Aa	1.35 Aa	1.40 Aa	1.40 Aa	1.31 Aa
T35 vs T25	1.15 Aa	1.62 Aa	1.53 Aa	1.46 Aa	1.11 Aa	0.96 Aa	1.10 Aa	1.27 Aa	1.30 Aa	1.20 Aa	1.42 Aa	1.44 Aa	1.27 Aa	1.29 Aa	1.29 Aa	1.36 Aa

Table S5. 3: Soil samples that were disturbed prior to incubation due to presence of large pumice gravel. None of the soil columns in site 1 were disturbed. Likewise, the topsoil layers up to 10 cm and 35-40 cm depth of all sites were not disturbed.

Site	Soil depth (cm)				
	10-15 cm	15-20 cm	20-25 cm	25-30 cm	30-35 cm
3	3B3, 3B3, 3B3, 3B3	3B4	3B5, 3B5, 3B5, 3B5	-	-
5	-	-	5C5, 5C5, 5C5, 5C5	5D6	-
7	7A3, 7A3, 7A3, 7A3, 7C3, 7C3, 7C3, 7C3,	7A4, 7B4, 7C4,	7A5, 7A5, 7A5, 7A5, 7B5, 7B5, 7B5, 7B5, 7C5, 7C5, 7C5, 7C5, 7D5,7D5, 7D5, 7D5	7A6, 7B6, 7C6	7A7, 7B7, 7C7

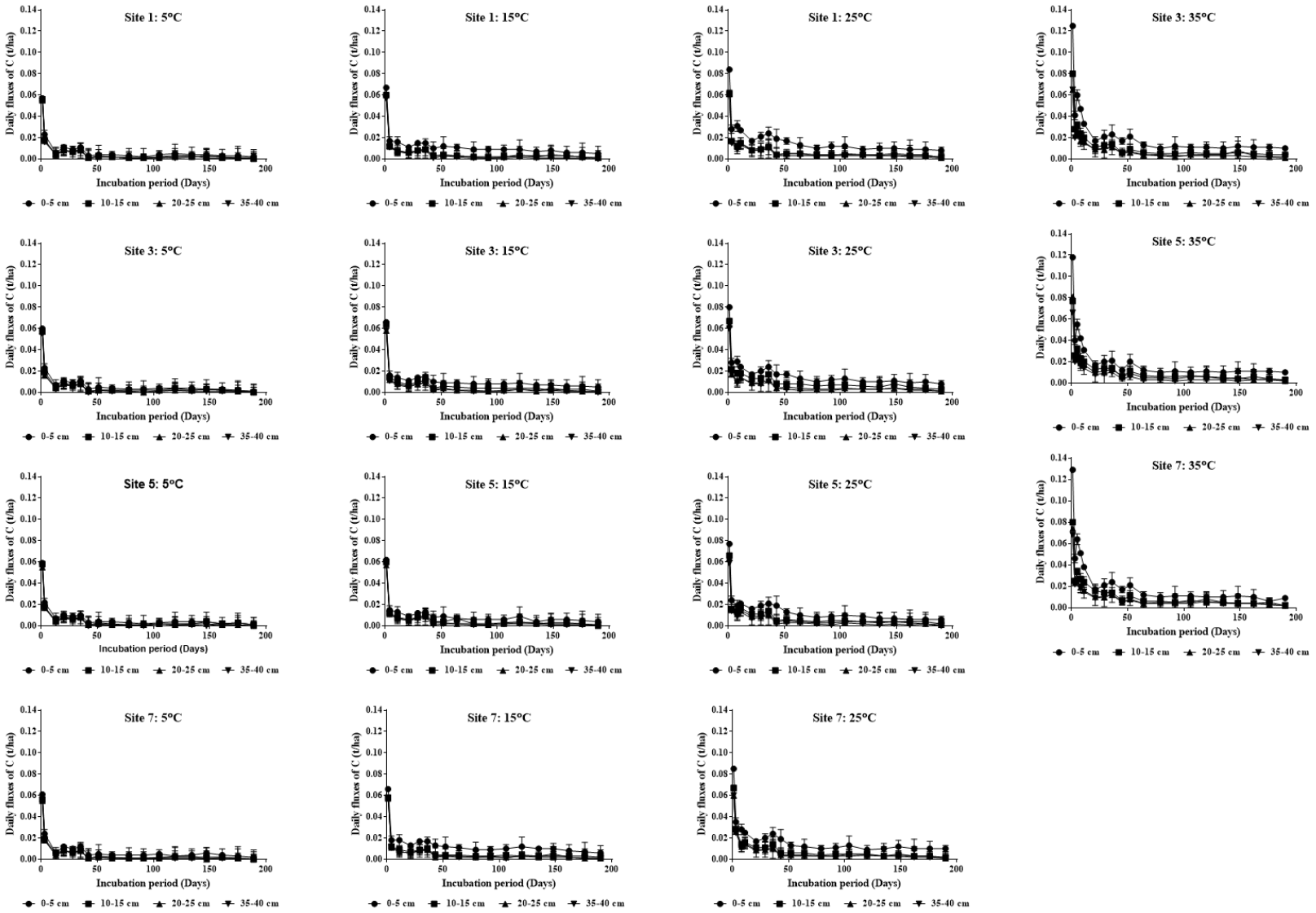

Figure S5. 1: Daily C fluxes (t/ha) and standard error of the mean at the different sites and temperatures for the 190 days incubation.

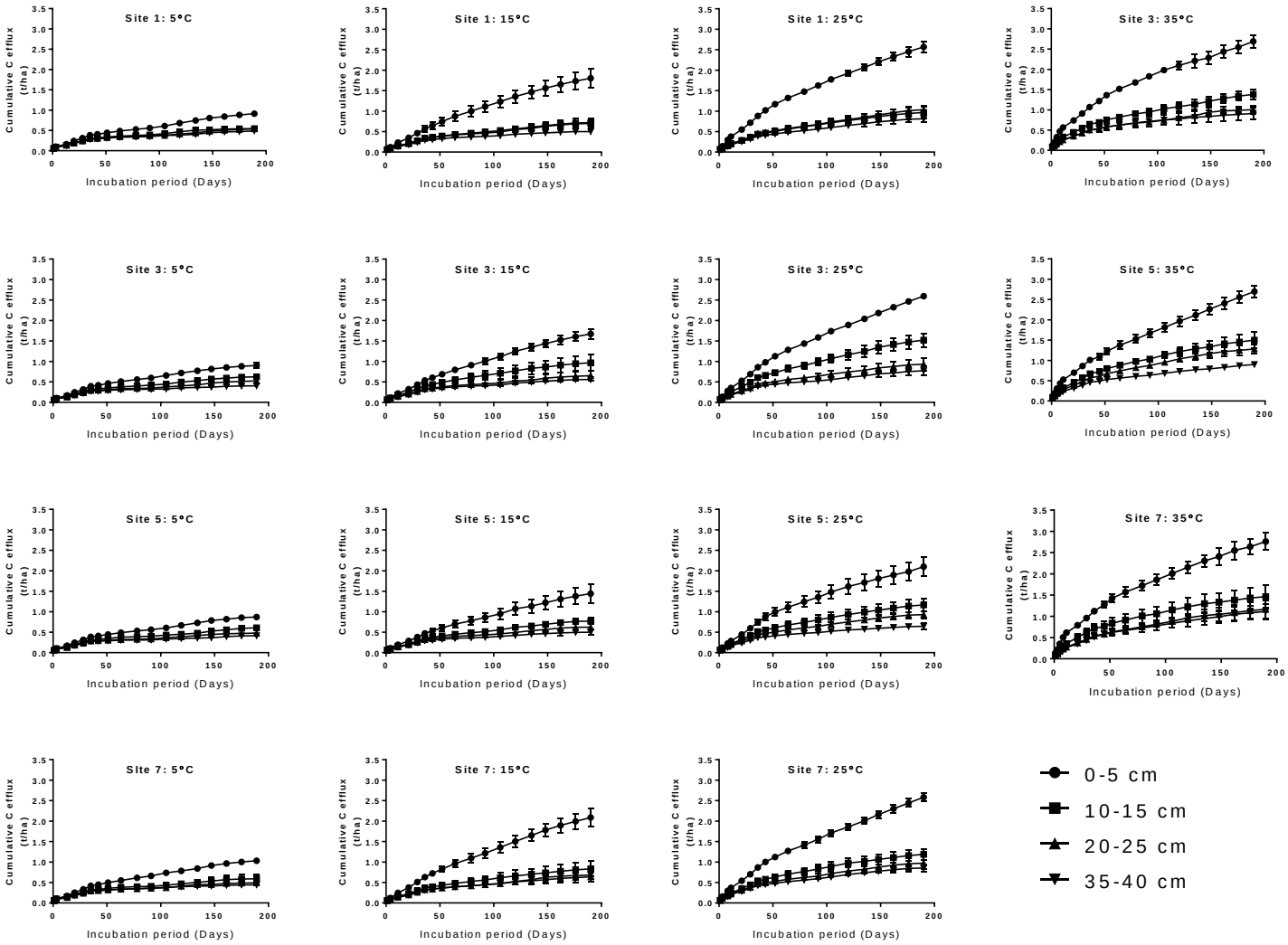

Figure S5. 2: Cumulative C efflux (t/ha) and standard error of the mean for the different depths and sites with the corresponding incubation temperatures for the 190 days incubation.

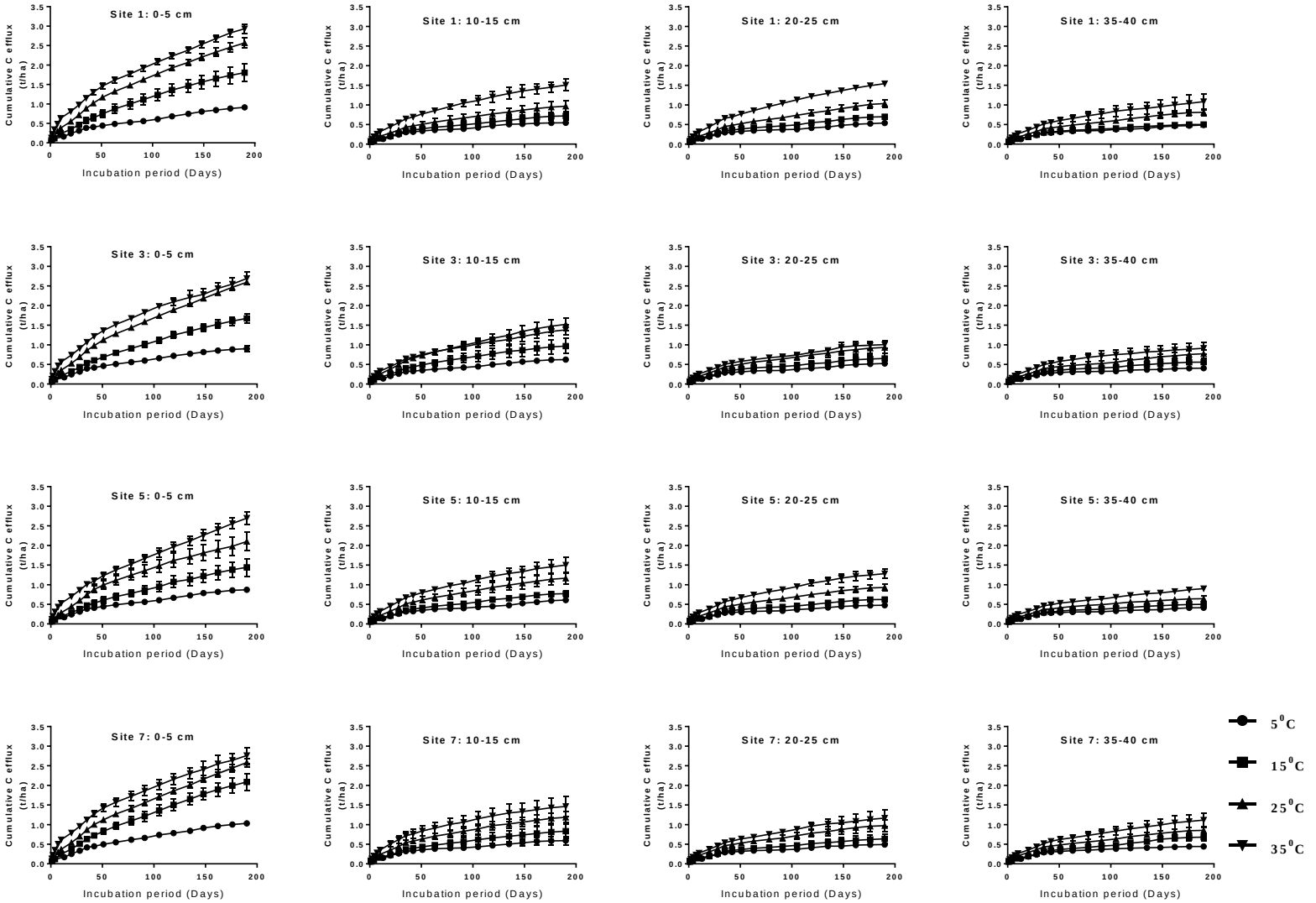

Figure S5. 3: Cumulative C efflux and standard error of the mean at each soil depth and sites with the temperatures of incubation.

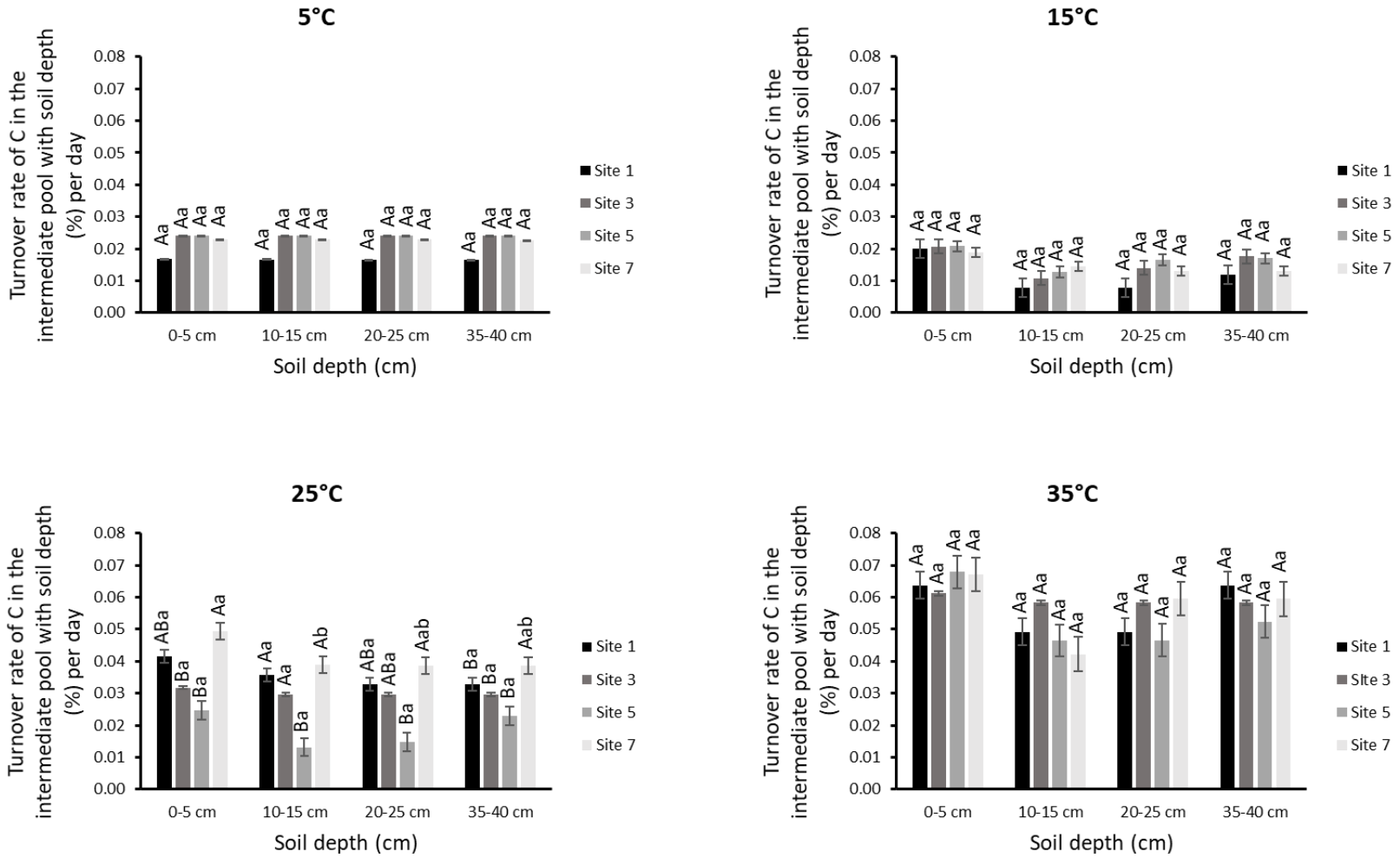

Figure S5. 4: Comparison of the influence of soil depth on the turnover rate of C in the intermediate pool at different temperatures from the three-pool model with constraints and standard error of the mean. Capital letters denote comparison between the four sites at the same depth (same letters mean not significantly different), small letters represent comparison of the four different depths at the same site under a given temperature (same letters mean depth was not significantly different at the corresponding site).

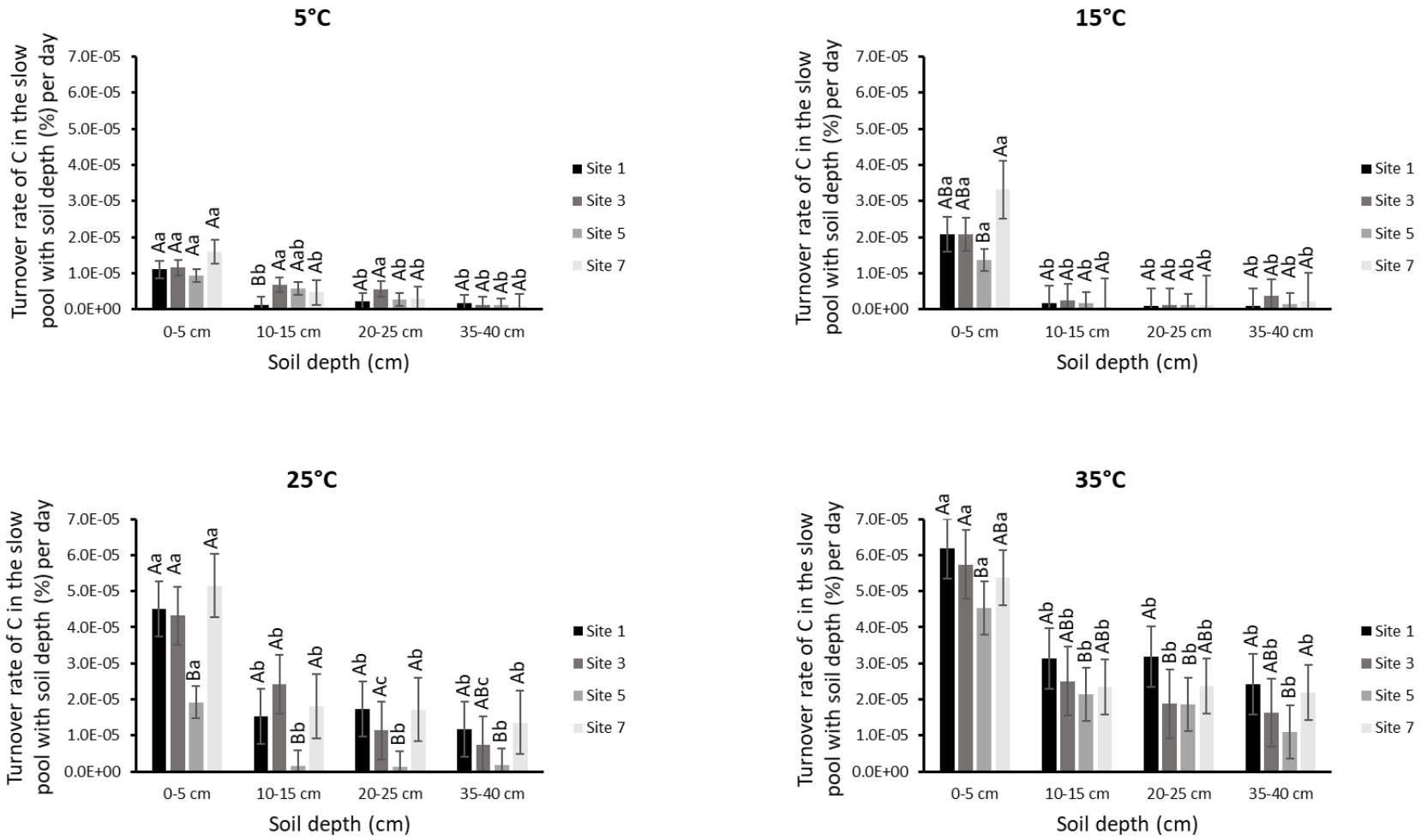

Figure S5. 5: Comparison of the influence of soil depth on the turnover rate of C in the slow pool at different temperatures from the three-pool model with constraints and standard error of the mean. Capital letters denote comparison between the four sites at the same depth (same letters mean not significantly different), small letters represent comparison of the four different depths at the same site under a given temperature (same letters mean depth was not significantly different at the corresponding site).

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