University of Zurich^UZH

The more the merrier? Influences of doubling litter inputs on carbon storage in a tropical forest

GEO 511 Master's Thesis

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Abstract

Stabilizing concentration of atmospheric CO_2 to diminish the risk of global warming is of great interest nowadays. As soil are not only a major store of carbon but also the largest source of carbon dioxide, they stimulate the interest for a better understanding of mechanisms of the carbon cycling and storage belowground. Hereby, tropical forest play an important role in the global carbon cycling and their response to environmental change will impact future concentration of atmospheric CO_2. Rising CO_2 concentrations in the atmosphere have led to an increase in aboveground NPP usually accompanied by increased litter inputs to the soil, leading to the assumption that many ecosystems will act as carbon sinks in the future. In this thesis, soil from a unique large-scale, long-term litter manipulation experiment in a tropical forest in Panama was examined to gain insight weather doubling litter inputs also lead to proportionate increases in soil organic carbon storage. The thesis shows that 15 years of litter manipulation treatment only led to minor increases of soil organic carbon with doubling litter inputs. Moreover, the small increase is not statistically significant and increases in litterfall due to increased CO_2 in the future will be less than the experimental doubling, indicating an overestimation of the already small net gains found. Further analysis showed that beside climatic conditions and soil chemistry, priming effects and the origin of soil organic carbon are possible explanations for the small net gains in soil carbon. These results show that soil organic carbon does not have a direct relationship with litter inputs to the soil and that soils will not act as carbon sinks in future climatic conditions, but they clearly highlight the importance of investigating plant-soil feedbacks regarding the predictions of carbon sequestration potential of tropical soils.

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Abbreviations

C	Carbon
^{13}C	Stable carbon isotope with atomic mass 13
CO_2	Carbon dioxide
DIRT	Detritus input and removal treatment
DOC	Dissolved organic carbon
FACE	Free air carbon dioxide enrichment
NPP	Net primary production
^{15}N	Stable nitrogen isotope with atomic mass 15
Pg	Petagramm = 10^{12} Kilogramm
Ppm	Parts per million
SOC	Soil organic carbon

1. Introduction

Soils are a major repository for carbon. They store more than twice as much as the atmosphere and the vegetation combined (Weil and Brady, 2017). In terms of terrestrial carbon, about 70% is stored in the world's soils (Catovsky et al., 2002). Soils are not only a major store of carbon, but also the largest source of carbon dioxide (CO_2) and consequently play an important role in the global carbon cycle, stimulating the interest for a better understanding of mechanisms of the carbon cycling and the storage belowground (Fahey et al., 2013; van Groenigen et al., 2017; Weil and Brady, 2017). This is especially important in the context of a changing climate because the carbon cycle is sensitive to environmental changes and vice versa: alterations in carbon cycling can affect our climate (van Groenigen et al., 2014). Therefore, stabilizing the concentration of atmospheric CO_2 to diminish the risk of global warming is of great interest (Lal, 2008). CO_2 concentrations in the atmosphere have increased since the start of the Industrial Revolution and will further increase in the future, leading to changes in the plant-soil feedback (Hartmann et al., 2013; Lal, 2008; van Groenigen et al., 2014; Weil and Brady, 2017). Despite extensive study of plant-soil feedbacks under elevated atmospheric CO_2 concentrations, the responses of soil carbon dynamics remain uncertain but play an important role when determining the potential of soils to act as sources or sinks of atmospheric CO_2 in future conditions (Jackson et al., 2017; Sayer et al., 2011; van Groenigen et al., 2017). Increases in CO_2 are expected to enhance net primary production (NPP), leading to a greater accumulation of organic matter on the floor (Sayer et al., 2011). But elevated atmospheric CO_2 levels can also stimulate microbial activity, resulting in higher soil respiration (Sayer et al., 2011; van Groenigen et al., 2014). It is therefore rather unclear how soil carbon storage will react to increased atmospheric CO_2 concentrations in the long term.

Great attention is paid to processes caused by increased NPP, as rising CO_2 concentrations in the atmosphere have led to an increase in aboveground NPP, and is expected to further increase in the future (Lewis et al., 2009; Pan et al., 2011; Sayer et al., 2011). This increase in aboveground NPP has led to the assumption that many ecosystems will act as carbon sinks, storing additional carbon from the atmosphere as biomass or incorporated in soils and therefore slow the rise of atmospheric CO_2 concentrations (Kuzyakov, 2011; van Groenigen et al., 2017). Especially forest soils are seen particularly promising for sequestering additional carbon because about 60% of the global terrestrial carbon sequestration occurs in forests (Bowden et al., 2014; Jackson et al., 2017; McKinley et al., 2011; Schlesinger and Lichter, 2001). Increases in NPP are usually accompanied by increased litter inputs to the soil and, if decomposition processes stay unchanged, this would lead to a proportionate increase of carbon stored in soils (Sayer et al., 2011). Even if many models generally assume a strong and direct relationship between NPP, litter inputs and soil carbon, there is little evidence for such a simple relationship (Jackson et al., 2017; Lajtha et al., 2018). The direct relationship between plant litter input and soil organic carbon is not well known, nor does it necessarily lead to direct or linear long-term changes in carbon storage in soils (Jackson et al., 2017, Lajtha et al., 2018). Numerous factors can contribute to non-linear relationships between litter inputs and soil carbon (Lajtha et al., 2018). For example, feedbacks like the priming effect, in which increased inputs of fresh organic matter stimulate the mineralization and release of stored soil carbon, could cause a disproportionate increase in soil CO_2 efflux, resulting in a smaller net gain or even a net loss in soil carbon storage (Sayer et al., 2011, Heimann & Reichstein, 2008). In addition, our understanding of the processes by which carbon is transformed within soils and exchanged with the atmosphere is limited (Heimann and Reichstein, 2008). Therefore, changes in plant-litter inputs have considerable potential to substantially affect carbon dynamics in forest soils, with possibly positive feedbacks to the atmospheric carbon levels, and need to be better investigated (Sayer et al., 2011).

1.1 Interactions of the global carbon cycle, terrestrial carbon pool and soil organic carbon

The element carbon is the basis for all life on Earth, as living tissues are made of carbon atoms arranged in chains or rings and combined with many other elements (Weil and Brady, 2017). The global carbon cycle describes the flow of carbon between a series of different carbon pools in the earth system. These pools, namely the atmospheric, terrestrial and oceanic pool, interact with each other via fluxes of carbon (Figure 1) (Ciais et al., 2013; Weil and Brady, 2017). The terrestrial carbon pool is the largest and can be further distinguished between vegetation and soils (Lal, 2008; van Groenigen et al., 2014). More than 70% of the terrestrial carbon is stored in soils, either as inorganic carbon in carbonates rocks or as soil organic carbon (SOC) in protected or unprotected forms (Catovsky et al., 2002; Weil and Brady, 2017). Soil organic carbon consists of plant and animal tissues at different stages of decomposition, bodies of living small animals and micro-organisms and their decomposing products, as well as microbiologically or chemically synthesized substances from breakdown products (Lal, 2008).

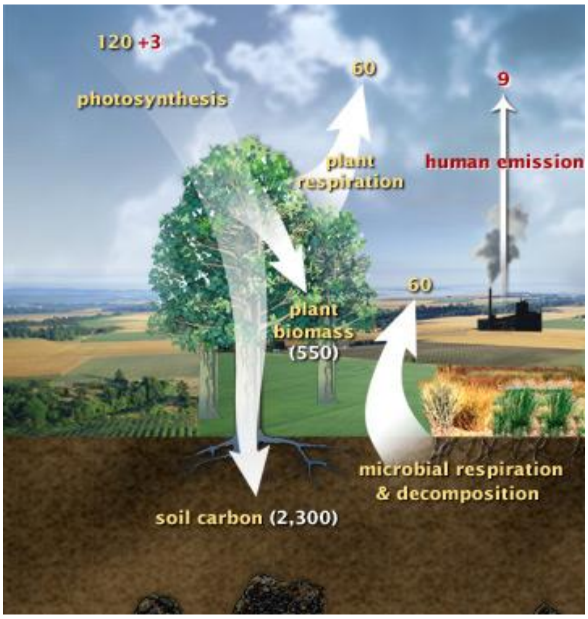

Figure 1. Graphic representation of the fluxes of carbon between land and atmosphere. White numbers indicate stored carbon, yellow numbers show natural fluxes and red numbers are human contributions. Fluxes are in gigatons per year (modified from Riebeek, 2011).

The atmospheric and terrestrial carbon pools interact with each other as plants take up CO_2 from the atmosphere via photosynthesis and carbon is stored as standing vegetation or root biomass. The vegetation again releases CO_2 to the atmosphere via plant respiration (Figure 1). Because of their dynamic relationship, the atmospheric carbon pool and the vegetation are key players in the global carbon cycle. Plant and root biomass then enters the soil as plant litter or root deposits (Weil and Brady, 2017). Once deposited on the soil surface, plant residues are decomposed and mineralized by soil organisms and carbon is respired back to the atmosphere, a term known as soil respiration (Figure 1). Therefore, soils are also a major source of CO_2 to the atmosphere, highlighting their fundamental role in the global carbon cycle (Batjes 1996; van Groenigen et al., 2014; Weil and Brady, 2017). Some of the carbon from partially metabolized plant tissue may be stabilized in soils via sorption and aggregation and is therefore protected from further decomposition for decades or even centuries (Six et al., 2002; Weil and Brady, 2017). Overall, the rate at which soil organic carbon storage increases or decreases depends on the balance between carbon gains and losses. Carbon inputs stem mainly from plant litter, root residues and root exudates, while losses occur due to respiration, erosion and leaching of dissolved organic carbon (DOC) (Weil and Brady, 2017). Several studies propose that carbon inputs to soils exceed efflux on a global scale and therefore, belowground carbon storage will increase and soils should act as carbon sinks in the short term (Ciais et al., 2013, Jones et al., 2005; van Groenigen et al., 2014).

1.2 Increased atmospheric CO_2 and its influence on plant-soil feedback

Since 1750, atmospheric CO_2 concentrations have increased by 40% and has now exceeded 400 parts per million (ppm). This increase is mostly human-induced, as it primarily stems from fossil fuel emissions and net land-use change emissions (Hartmann et al., 2013). Different climate models (Figure 2) indicate that the CO_2 concentration will further rise in the future. Atmospheric CO_2 concentrations could rise to 1000 ppm by the end of the century (Collins et al., 2013).

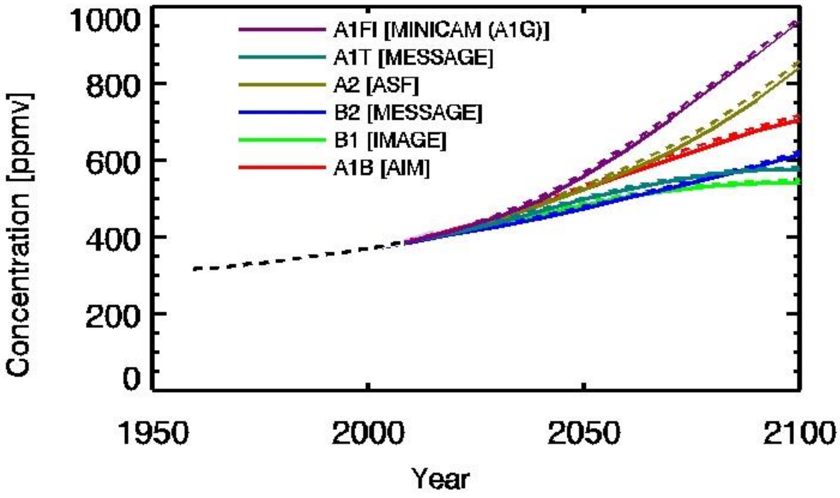

Figure 2. Atmospheric CO_2 concentrations measured at the Mauna Loa Observatory from 1958 to 2008 (black dashed line) and projected future increases in atmospheric CO_2 under six different scenarios; two global carbon cycle models were used for each scenario (solid and dashed line; source: IPCC Data Distribution Centre).

Increased CO_2 in the atmosphere leads to changes in the plant-soil feedback as the carbon dynamics between the terrestrial and atmospheric carbon pools are very sensitive to environmental changes (Hartmann et al., 2013; Lal, 2008; van Groenigen et al., 2014; Weil and Brady, 2017). As NPP is not saturated at ambient atmospheric CO_2 levels, increasing atmospheric CO_2 concentrations are expected to boost aboveground NPP, as plants take up additional CO_2 from the atmosphere via photosynthesis (Lal, 2008; Sayer et al., 2011). This, in turn, influences the amount of soil organic matter accumulated in soils, as the NPP provides plant tissue, which is the original source of soil organic matter (Batjes, 1996; Weil and Brady, 2017). It follows that, if the previously described decomposition processes stay unchanged, greater litter inputs to the soil would lead to a proportionate increase of carbon stored in soils (Sayer et al., 2011). This would be a direct and strong relationship, which is also generally assumed in earth system models, resulting in the assumptions that soils will act as carbon sinks in the future (Jackson et al., 2017; Lajtha et al., 2018). However, the accumulation of carbon in the soil also stimulates soil microbial activity and increases soil respiration, which in turn enhances carbon efflux from the soil to the atmosphere (Batjes 1996; van Groenigen et al., 2014; Weil and Brady, 2017). Inputs of carbon into the soil during the decomposition of plant litter and the release of carbon as CO_2 through microbial activity are normally balanced in a mature natural ecosystem (Weil and Brady, 2017). However, the carbon balance of terrestrial ecosystems can be markedly changed by increased atmospheric CO_2 concentrations (Batjes, 1996). Moreover, carbon dynamics in soils are not well understood and direct effects of changes in the quantity of litter on soil carbon balance remain poorly understood. Therefore, it remains unclear how changes in CO_2 concentrations in the atmosphere affect soil carbon storage via changes in NPP (Fekete et al., 2014; Jackson et al., 2017; Lajtha et al., 2018; van Groenigen et al., 2014).

1.3 Litter manipulation experiments

Litter manipulation experiments can improve our understanding of carbon dynamics in soils by simulating the increased litter inputs as a result of enhanced NPP under elevated atmospheric CO_2 concentrations. The goal of such litter manipulation experiments is to assess how the accumulation, dynamics and stabilization of organic matter and nutrients is controlled by the rate and source of plant litter inputs over decadal time scales (Lajtha et al., 2018; Nadelhoffer et al., 2004). The first detrital input and removal treatment (DIRT) was designed and started by Francis D. Hole in the United States in 1956. The design included treatments altering aboveground litter and root inputs to soils. Inspired by the design of Francis D. Hole, many more litter manipulation experiments were established around the globe, mainly in the temperate zone (Nadelhoffer et al., 2004). The design is simple and can include several treatments (Table 1, Figure 3).

Table 1. Different possible treatments for litter manipulation experiments; adapted from Nadelhoffer et al. 2004.

Treatment	Manipulation
Control	Normal litter inputs, undisturbed
No Litter	Aboveground litter is removed
Double Litter	Twice the normal aboveground litter input
No Roots	Roots excluded by lined trenches
No Inputs	No aboveground litter and no roots

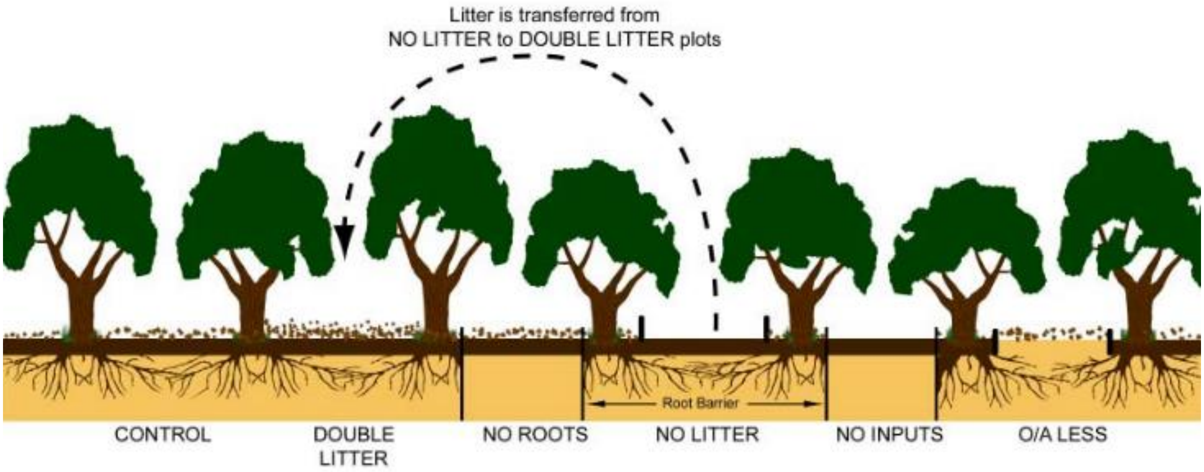

Figure 3. Conceptual diagram of a detritus input and removal experiment; dark brown is the organic horizon, light brown shows the mineral soil (from Nadelhoffer et al., 2004).

Results of such DIRT-Experiments provide no evidence to date for either a linear or a direct relationship of litter inputs and carbon stored in soils. Although litter removal generally resulted in a decrease of carbon stored in soils, double litter inputs did not necessarily lead to increased soil organic carbon but rather showed variable results across the sites, indicating the need to investigate how soil carbon dynamics are linked with litter inputs (Lajtha et al., 2018).

1.4 This Master's Thesis

In this master's thesis, I focus on a long-term experiment in a tropical forest in Panama, in which aboveground litter inputs have been manipulated since 2003. In this experiment, Emma Sayer and her team discovered that the efflux of CO_2 derived from soil organic carbon was significantly increased by litter addition after six years of treatments, which they attributed to priming effects (Sayer et al., 2011). They predicted that a future increase of 150 ppm CO_2 in the atmosphere would lead to an increase in litterfall of 30%, releasing 0.6t C ha^{-1} yr^{-2} from the soil (Sayer et al., 2011), which would partially offset predicted net gains in carbon storage. The aim of this thesis was to measure and calculate soil organic carbon concentrations and stocks in the experimental plots at different depths after 15 years of continuous litter addition treatments. Litter removal treatment across various litter manipulation experiments showed the same results. Therefore, and because the litter removal treatment is highly unrealistic, I am only interested and only investigate the impacts of doubling litter inputs on soil organic carbon content. My study will provide an insight into whether the observed increased soil respiration due to priming effects has offset soil carbon storage, which in turn would create a positive feedback to climate change. I therefore aimed to address the following research questions:

Does doubling litter inputs in a tropical forest increase carbon storage in soil?
At which depth increments is soil carbon storage most affected by altering litter inputs?

Such studies in tropical forests are rare, and to my knowledge, there is only one other experiment in Costa Rica (Leff et al. 2012), which was short-term, making the long-term manipulative experiment in Panama unique for the tropics. Nonetheless, about 30% of the global carbon stocks are stored in the tropics and they play a fundamental role in the global carbon cycle (Jobbágy and Jackson, 2000). Moreover, tropical forests are characterized by a fast carbon turnover rate, but the carbon sequestration capacity of tropical forest soils is uncertain and plant-soil feedbacks on soil carbon dynamics are not fully understood, indicating the need to investigate carbon dynamics in the tropics (Jackson et al., 2017; Sayer et al., 2007; Tanner et al., 2016).

2. Methods

2.1. Study site and experimental design

The study was conducted as a part of an ongoing long-term and large-scale litter manipulation experiment in a tropical forest in Panama. The forest under study is an old-growth mature lowland semi-evergreen tropical forest, situated on the Gigante Peninsula (9°06'N, 79°54'W) of the Barro Colorado Nature Monument in Panama (Sayer et al., 2007; Sayer et al., 2011). The soil is described as an Oxisol, which is highly weathered, characterized by a pH of 4.5 – 5.0, low available phosphorus concentrations but high base saturation and cation exchange capacity and kaolinite as the dominant clay mineral (Baillie et al. 2006; Sayer et al. 2006; Tanner et al. 2016; Weil and Brady 2017). Barro Colorado Island, which is about 5 km from the study site, receives a mean annual rainfall of 2600mm, with a strong dry season from January to April. Approximately 90% of the annual precipitation occurs during the rainy season. The average temperature on Barro Colorado Island is 27°C (Leigh 1999; Leigh and Wright 1990).

In 2000, fifteen 45-m x 45-m plots were established within a 40-ha area of forest. To minimize lateral nutrient- and water movement via roots or mycorrhiza network, all 15 plots were trenched to a depth of 0.5 m. The trenches were double-lined with plastic and backfilled (Figure 4). Litter manipulation started in January 2003. In five plots, litter (including branches ≤ 100mm in diameter) was raked up monthly, resulting in low but not entirely absent litter standing crop (litter removal plots). The removed litter was instantly spread out as evenly as possible on five further plots, doubling the monthly litter inputs (DL plots). Five plots were left undisturbed as controls (CT plots; Figure 4) (Sayer et al., 2006; Sayer et al., 2007). The plots were geographically blocked. Litter from a particular litter removal plot was always added to a particular double litter plot and the nearest control plot completed each block (Tanner et al., 2016). A location map of the plots can be seen in Figure 5.

Soil samples were collected after 15 years of continuous monthly treatment in May 2018 with a hand corer in the double litter and control plots. To avoid trenching effects, all samples were taken within a 30-m x 30-m buffer zone. Samples were taken at three different depth increments: 0-10 cm, 10-20 cm, 20-30 cm at three random sampling points per plot, resulting in a total of 90 samples (10 plots x three sampling points x three depths) The soil cores were air-dried within eight hours of collection, individually wrapped in aluminum foil, sealed in plastic bags and transported to the laboratory at the University of Zurich.

Figure 4. Photograph of the litter manipulation plots in the study forest in Panama, Central America; on the left is the double litter treatment, on the upper right the control treatment, and at the bottom right is the litter removal treatment; the black plastic shows the location of the back-filled trenches between adjacent plots (photo by E. Sayer).

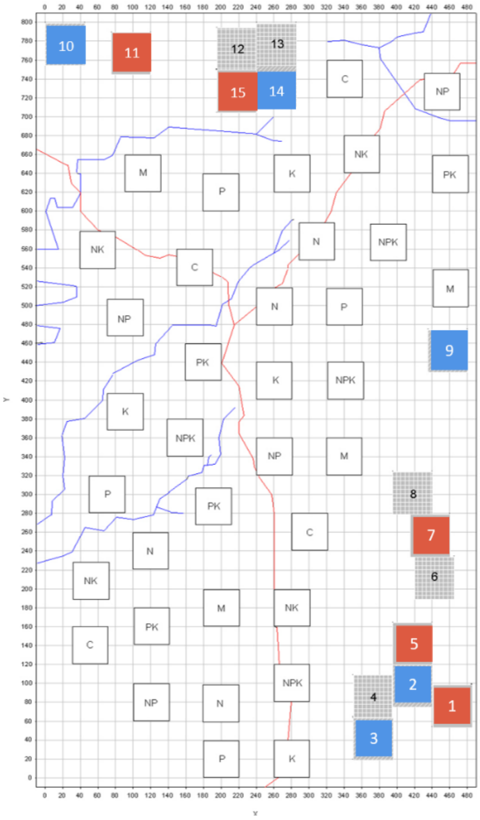

Figure 5. Map showing the location of the experiment plots within a 40-ha area of lowland tropical forest in Panama, Central America. Each double litter plot (blue) has a corresponding litter removal plot (grey) and a nearby control plot (orange); white squares denote the location of an adjacent fertilisation experiment (map modified from Sayer 2005).

2.2. Laboratory analysis

Laboratory analysis was done at the Geography Department of the University of Zurich. Dried soils were sieved with a 2-mm mesh sieve to separate stones and roots from the soil. The roots were weighed separately to get an insight into the fine root distribution. Subsamples of approximately 10 g were finely ground and homogenized with a horizontal swing mill (MM400 © Retsch) for 40 seconds and a frequency of 30 hertz, using one ball.

2.2.1. Elemental Analysis

To determine total organic carbon and nitrogen content, sieved and milled soil samples were analyzed with an elemental analyzer including isotope ratio mass spectrometry (EA-IRMS; Thermo Scientific™EA-IRMS Delta V ™Plus). Two analytical replicates of *c.* 5 mg dry weight for each soil sample were weighed into tin capsules using a Micro Scale (Cubis MSU 6.6S-000-DM © Sartorius). The capsules were carefully closed and put into the EA-IRMS, where they are combusted at a high temperature. Flooding with pure oxygen leads to complete combustion into CO_2 and NO_x. The resulting gases are measured by means of thermal conductivity, resulting in percent values of total carbon and total nitrogen content (Muccio and Jackson, 2009). With a low soil pH of 4.5 – 5.0 we can assume that there is no inorganic carbon present, which is typical for a tropical soil, and the absence of inorganic carbon has been confirmed by Bailie et al. (2006). Due to this absence of inorganic carbon, the measured total amount of carbon corresponds to the total amount of soil organic carbon (SOC) (Schumacher, 2002). Values for $\delta\ ^{13}C$ and $\delta\ ^{15}N$ were then obtained using isotope ratio mass spectrometry (see Muccio and Jackson (2009) for more information). $\delta\ ^{13}C$ values are mainly used to reveal insights of vegetation changes, while $\delta\ ^{15}N$ values allow you to draw conclusions about the development of decomposition. It is noteworthy however, that isotopic fractionation processes in soils are mostly complex and affected by a combination of factors, such as soil mineralogy and chemistry, vegetation, clay content and pH (Krull and Skjemstad, 2003).

2.3. Estimating soil carbon stocks

Soil organic carbon stocks were estimated by multiplying the measured organic carbon content by bulk density and depth of the respective soil layer. Due to the absence of stones, no correction factor was used (Poeplau et al., 2017). The calculations were done in Excel 2013.

For 0-10 cm depth, I obtained bulk density data from Rodtassana (2016). They measured soil bulk density from five soil cores per plot at two depths (0-5 cm and 5-10 cm). Soil cores were taken monthly over a year (March 2013 – February 2014) to capture differences in wet and dry season. Mean values per plot were then calculated as 0.54 ± 0.08 g cm^{-3} for control plots and 0.54 ± 0.08 g cm^{-3} in double litter plots.

As bulk density data below 10 cm depth does not vary across the site and time, bulk density data from one pit was used across all plots. Data from four soil pits showed that the coefficient of variation for bulk density at 10-20 cm was *c*. 10% and at 20-50 cm depth it was *c*. 3% (Tanner et al., 2016). Therefore, I used bulk density data from the pit closest to the litter manipulation plots for the 10-20 cm increment (0.86 g cm^{-3}), and the means of two soil pits for the 20-30 cm (1.06 g cm^{-3}) to estimate soil organic carbon stocks (Rodtassana, 2016; Tanner et al., 2016).

2.4. Statistical Analysis

Data analyses were carried out in R version 3.3.2 (R Core Team 2016). The data were first visually explored to check their distribution. For quality controls of the carbon content data, mean values of the analytical replicates were calculated, as well as the relative standard deviation. Whenever the relative standard deviation exceeded 10%, new analytical replicates were measured. The C:N ratio was calculated using the values of carbon and nitrogen to reveal insights of litter quality. Plant residues with a high C:N ratio are generally harder to decompose for the microbes compared to plant residues with a low C:N ratio. Moreover, a narrow C:N ratio is a sign of advanced decomposition (Weil and Brady, 2017).

All data were checked for the normality of the distribution with histograms and tested for normality (*shapiro.test* function) and the data were log transformed when necessary to achieve normally distribution.

To asses if the mean values of any of the measured variables differed between the double litter treatment and the control, t-tests were used *(t.test* function). The difference between the two treatments was regarded as statistically significant if the p-value was < 0.05. Additionally, a linear model (*lm* function) was used to asses treatment and depth effects on soil organic carbon. Where mean values of the plots or treatments are given, the standard error was used in order to indicate how precisely the estimate of the mean value is.

3. Results

3.1. Elemental concentrations

Elemental analysis showed that values for soil organic carbon content in the soil under study ranged from 12.3 g C kg^{-1} to 50.5 g C kg^{-1} and decreased with soil depth (Figure 6a). The same pattern was observed for soil nitrogen content, which ranged between 1.1 g N kg^{-1} and 4.6 g N kg^{-1}, and also decreased with depth (Figure 6b). The soil C:N ratio ranged between 10.1 and 11.6, with mean C:N ratios for both treatments around 11 (Figure 6c).

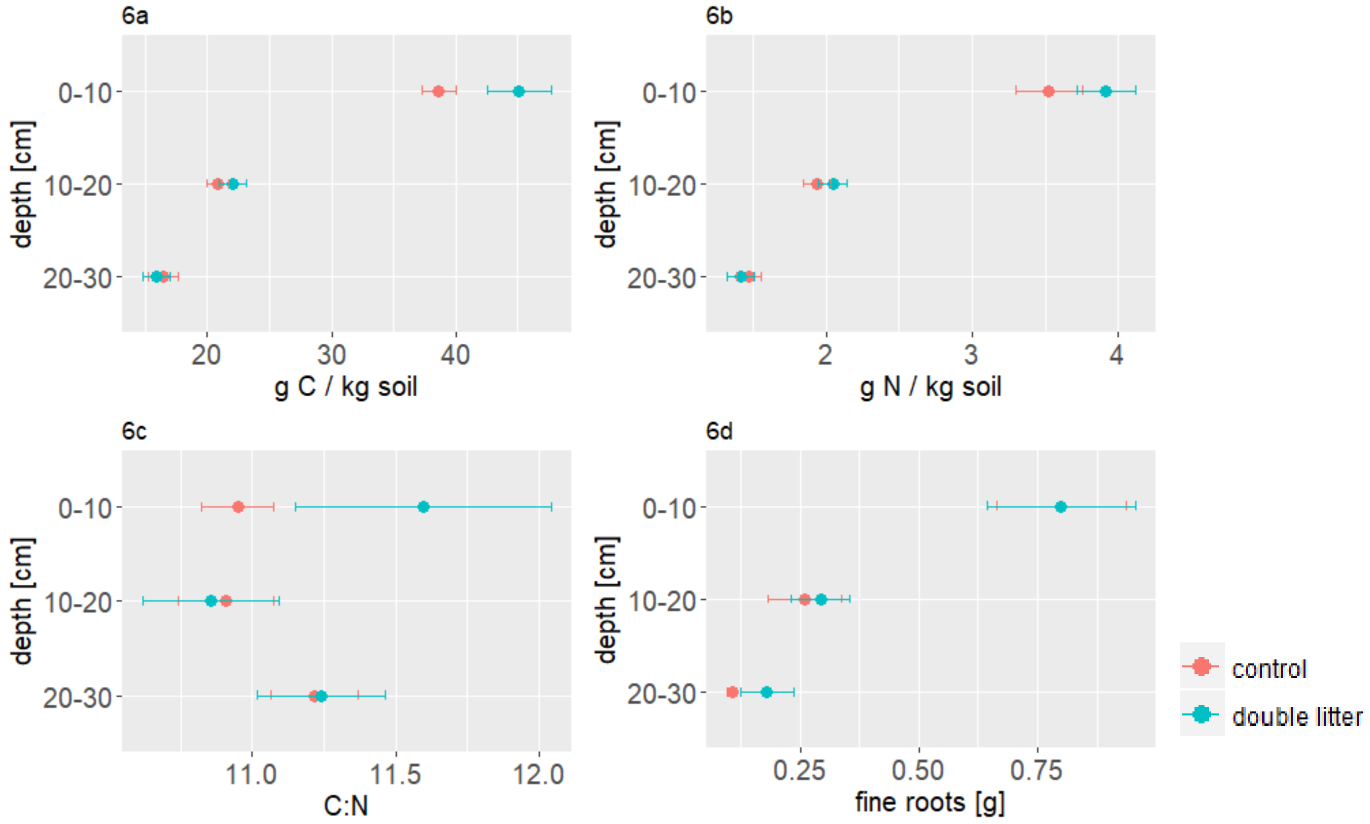

Figure 4. Soil organic carbon (C), nitrogen (N), C:N ratio and mass of fine roots at different depths in litter manipulation plots in a lowland tropical forest in Panama, Central America; where orange is the control treatment and blue is the double litter treatment, showing means and standard error bars for *n*=5 per treatment and depth.

3.1.1. Soil organic carbon concentrations increased with double litter input

Statistical analysis revealed that after 15 years of litter manipulation treatment, soil organic carbon content to 30-cm soil depth had increased by *c*. 9.4% in the DL plots (27.69 ± 2.7 g C kg^{-1} soil) compared to the control plots (25.31 ± 3.4 g C kg^{-1} soil; Figure 7) but the increase was not statistically significant (p = 0.699). The biggest difference in soil organic carbon was observed at 0-10 cm depth (Figure 6a), where soil organic carbon content had increased by *c*. 16.8% in the DL plots (45.14 ± 1.4 g C kg^{-1} soil) relative to the controls (38.64 ± 2.6 g C kg^{-1} soil; p=0.071. At 10-20 cm depth, soil organic carbon increased by *c*. 5.8% in DL plots, and by *c*. 3.4% at 20-30 cm depth, showing that the difference of soil organic carbon concentration between double litter and control treatment decreased with depth (Figure

6a). A linear model confirmed this trend, showing that depth had a greater influence on soil organic carbon than treatment.

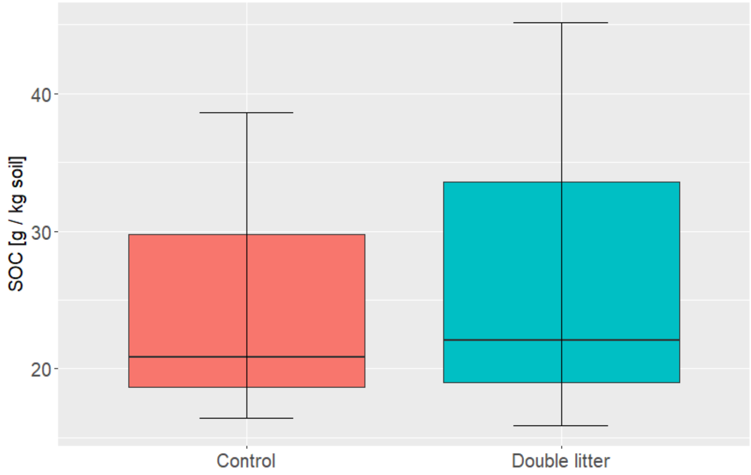

Figure 5. Distribution of soil organic carbon measurement in litter manipulation plots in a lowland tropical forest in Panama, Central America; where orange is the control treatment and blue is the double litter treatment. The boxes show the interquartile range, the black lines inside the boxes represent the medians.

Additionally, a pair-wise comparison between the double litter plot and the corresponding control plot was made (see Figure 5 in Methods 2.1). Only one pair (5C and 2L+, see appendix A) showed a statistically significant difference between treatments at a depth of 0-10 cm (p=0.005). In all other pairs and depths, no difference between double litter plots and control plots were revealed, confirming the results of the mean value comparison.

Although there was no significant difference in the mass of fine roots between double litter plots with control plots, the difference between treatments tended to increase with depth (Figure 6d). As the mass of fine roots in both treatments decreased with depth it was strongly correlated with soil organic carbon content (r=0.787; Figure 8).

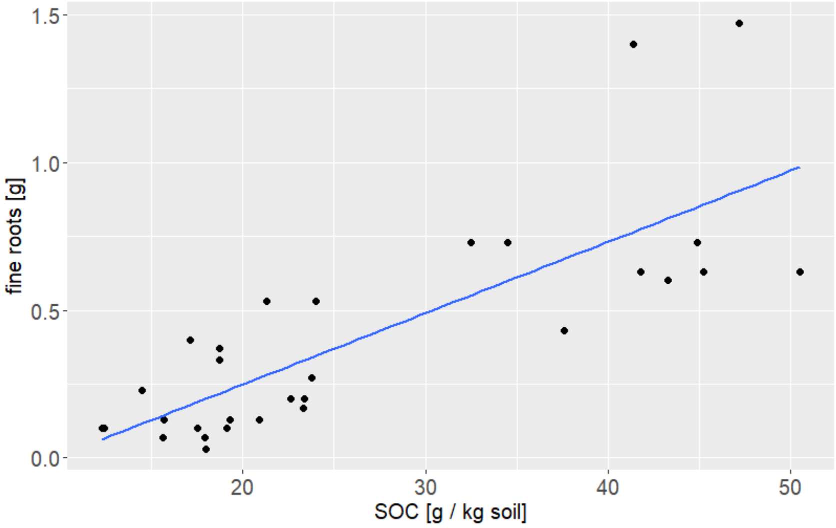

Figure 6. Relationship between SOC content and the mass of fine roots in the soil at 0-30 cm depth in a lowland tropical forest in Panama, Central America. Black points are individual values (one value per plot and depth (0-10 cm; 10-20 cm; 20-30 cm), r^2 = 0.787.

3.1.2. Nitrogen content does not significantly differ between treatments

Values of nitrogen concentrations show the same trends as soil organic carbon, whereby concentrations decreased with depth, as did the differences between treatments (Figure 6b). Again, differences between double litter and control were not statistically significant. Comparing nitrogen concentrations with measurements done in 2008, nitrogen content did not change over the period and shows a similar range (1.1-4.6 g N kg^{-1}).

3.1.3. No clear trend for C:N ratio

As there was no significant difference between treatments for either carbon or nitrogen concentration, it is not very surprising that the C:N ratio did not vary significantly between double litter and control plots. The mean C:N ratio for the control treatment was 11.05, which is only very slightly lower than the C:N ratio in the double litter plots (11.12). However, the trends in the C:N ratio with depth did not match the patter of elemental concentrations, as the C:N ratio changed very little with depth and showed no clear trend (Figure 6c).

3.2. Soil organic carbon (SOC) stocks are slightly higher in double litter plots

Soil organic carbon stocks for 0-10 cm depth were calculated using bulk density values measured in 2013-2014 by Chadtip Rodtassana. Bulk density at this depth increment ranged from 0.47 g cm^{-3} to 0.66 g cm^{-3} and did not differ significantly between double litter and control plots, with mean values of in 0.56 ± 0.01 g cm^{-3} for control plots and 0.55 ± 0.02 g cm^{-3} in double litter plots. For 10-20 cm and 20-30 cm increments, the same bulk density estimates were used for both treatments, because there is no difference in bulk density below 10 cm depth (Tanner et al., 2016; see Chapter 2.3 in Methods). Consequently, soil organic carbon stocks did not differ significantly between treatments at any depth interval. The highest soil organic carbon stocks were found in the uppermost layer, with 21.74 ± 1.36 t ha^{-1} for control plots and 24.87 ± 2.82 t ha^{-1} for double litter plots and decreased slightly with depth in both treatments (Figure 9). The double litter plots had slightly higher soil organic carbon stocks to a depth of 20cm, whereas the control plots had higher stocks at 20-30 cm depth, with 17.47 ± 1.11 t ha^{-1} compared to 16.92 ± 2.53 t ha^{-1} in double litter plots. However, none of the differences were statistically significant. Overall, soil organic carbon stocks for 0-30 cm depth were 57.17 ± 2.58 t ha^{-1} in control plots and 60.77 ± 2.54 t ha^{-1} in the double litter plots with, which represents a non-significant increase of *c*. 6.3% after 15 years of litter addition treatments (Figure 9).

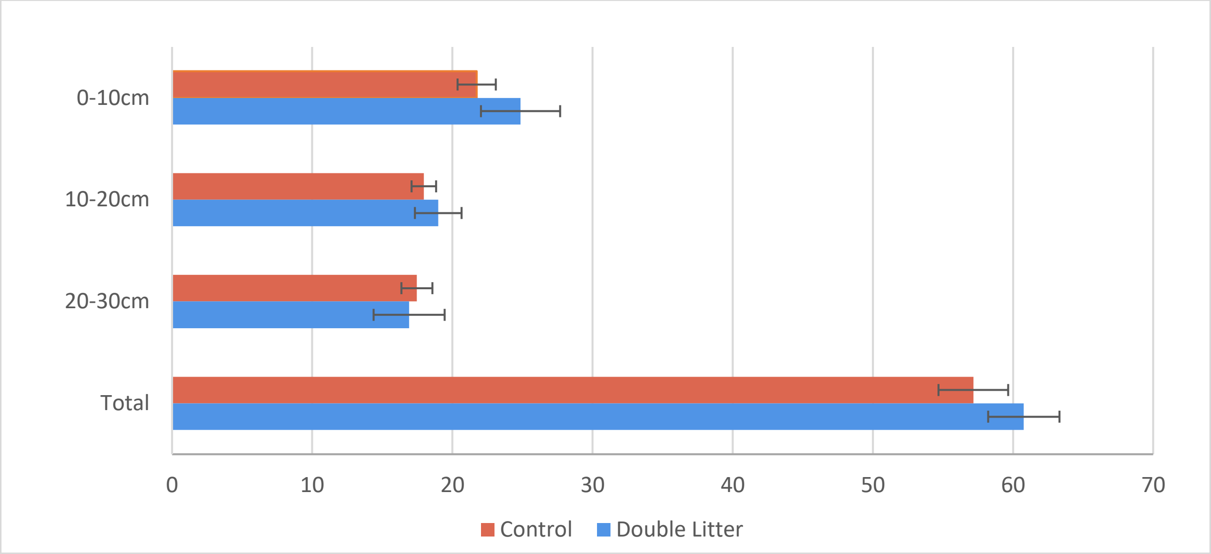

Figure 7. Soil organic stocks [t/ha] per depth for three depth increments and over the whole soil profile from 0-30 cm depth in litter manipulation plots in a lowland tropical forest in Panama, Central America; where red is the control treatment and blue is the double litter treatment. Error bars indicate the standard error, n = 5 per treatment and depth, n=15 per treatment in total.

3.3. Isotopic values of soil carbon and nitrogen

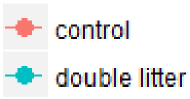

Figure 8. Isotopic values soil carbon (delta ^{13}C) and soil nitrogen (delta ^{15}N) at different depths in litter manipulation plots in a lowland tropical forest in Panama, Central America; where orange is the control treatment and blue is the double litter treatment, showing means and standard error bars for *n*=5 per treatment and depth.

Isotopic values for δ ^{13}C and δ ^{15}N were measured in the same process as the elemental concentrations. The δ^{13}C values ranged between -28.12‰ to -24.61‰ over both treatments (Figure 10a), which is close to the typical range for C_3 plants that dominate at the site (Emma Sayer, personal communication). There were no significant differences between double litter and control treatments at any depth. The lowest δ^{13}C values were found in the uppermost layer (0- 10 cm) and the values increased with depth (Figure 10a).

The values for $\delta^{15}N$ showed a similar pattern to $\delta^{13}C$; the values ranged between 4.3‰ to 8.0‰ with the lowest values at 0-10 cm, increasing with depth (Figure 10b). There were no significant differences between treatments at any depth.

4. Discussion

4.1. Discussion of the values

Looking at the data, we can find similar trends for different elements and values within the study. Soil organic carbon, nitrogen and fine roots all decrease with increasing depths in both the double litter and the control plots (Figure 6a, 6b and 6d). We can therefore say that doubling litter input does not change the distribution of the elements with depth. Both the soil organic carbon and the nitrogen values were also in a similar range as measurements done at the same site and can be taken as reliable (Grimm et al., 2008; Sayer et al., 2012; Tanner et al., 2016).

A similar trend could be found for the isotopic values of δ ^{13}C and δ ^{15}N. Both values increase with depth in the double litter and the control plots (Figure 10a and 10b). The enrichment in ^{13}C with depth is seen in most soils and is due to soil-inherent and decomposition processes. During decomposition, soil microorganisms fractionate ^{13}C and add ^{13}C enriched microbial biomass, indicating that decomposition of soil organic carbon is more advanced in deeper soil layers (Krull and Skjemstad, 2003). The enrichment of ^{15}N with depth also shows that more decomposed material can be found in deeper soil layers, confirming the results of the δ ^{13}C analysis. This trend and also the values are consistent with an analyzed Oxisol in Australia and can therefore be taken as reliable (Krull and Skjemstad, 2003). Concluding we can say that both isotopic values show that more decomposed material can be found in deeper soil layer, however, there is no statistically significant difference between the double litter plots and the control plots.

The only value showing no clear trend is the C:N ratio (Figure 6c). Nevertheless, the ratio shows the same behaviour with depth for both treatments. In the first 20cm, C:N ratio tends to narrow, which is a sign of advanced decomposition (Johnson et al., 1995; Krishna and Mohan, 2017; Krull and Skjemstad, 2003). After 20cm though, C:N ratio is again increasing, indicating that soil organic carbon at this depth may still contain comparatively labile components. This trend was also found in an analysis of an Oxisol in Beechmont (Queensland, Australia) by Krull and Skjemstad (2003).

4.2. There is only a small increase in soil organic carbon…

Although soil organic carbon increased by *c.* 16.8% in the double litter plots compared to the controls in the upper 10 cm of the soil, the increase was not significant, even after 15 years of treatment. Indeed, none of the differences between double-litter and control treatments were statistically significant at any of the depth increments, and over the whole soil profile. In fact, the *c.* 16.8% increase is smaller than we would expect after 15 years of double monthly litter inputs. Moreover, soil organic carbon stocks over 0-30 cm soil depth increased by only *c.* 6.3%.

Similarly small increases in soil organic carbon were also found by other scientists working at the same site (Tanner et al., 2016; Sayer et al., unpublished). My results for the upper 10 cm of the soil are within the same range as those reported in other studies: Sayer et al. (unpublished) reported an increase of 11%

after 13 years of litter manipulation, whereas Tanner et al. (2016) detected a difference of 14% within 6 years after the start of the experiment.

4.2.1. … compared with other studies

Widening the scope, there is only one other litter manipulation experiment in a tropical forest. In a study conducted in a wet tropical forest in Costa Rica by Leff et al. (2012), a much stronger effect of doubling litter inputs was observed. Soil organic carbon increased by 31% after only 2 years of doubling litter inputs in 0-10 cm. Already after 1 year of treatment, they found significant differences between double litter and control plots (Leff et al., 2012). The apparent difference in magnitude and rate of soil carbon response is noteworthy because soils underlying tropical forests contain about 20% of the world's soil organic carbon (Jobbágy and Jackson, 2000; Leff et al., 2012).

Table 2. Comparison of two experimental sites in tropical forests (data from Leff et al., 2012 and Sayer et al., 2011).

	Costa Rica	**Panama**
Duration	2 years	15 years
Size	3-m x 3-m	45-m x 45-m
Annual precipitation	4430 mm	2400 mm
Mean annual temperature	25°C	27°C
Soil classification	Highly weathered clay Utisol	Oxisol (high clay content, but low activity type)

Studies in temperate zones also found no consensus whether increasing litter inputs leads to enhanced carbon sequestration or not with different litter manipulation experiments showing highly variable results. Some scientists found an increase in soil organic carbon while some of them observed no changes or even a decrease in soil organic carbon (Bowden et al., 2014; Lajtha et al., 2014, 2018; Pisani et al., 2016; Xu et al., 2013).

There are several factors that can contribute to these differences in the strength of the effect. First, the two experimental sites in the tropics differ in terms of spatial scale, with much smaller plots in Costa Rica than in Panama (Table 2). These small pots can be “hot” or “cold” spots compared to large individual tree crown areas (commonly 25 m in diameter), and consequently tree root areas. Therefore, these small plots may not represent adequately what would happen in plots the size of large trees (Tanner et al., 2016), particularly as hotspots with large inputs of nutrients and organic matter can stimulate fine root proliferation (Sayer et al. 2006 and references therein), which would increase soil carbon inputs belowground. Moreover, the site in Costa Rica receives about the double amount of rainfall (Table 2).

This is important because increases in mineral soil carbon can be a result of greater infiltration of dissolved organic carbon (DOC) with double litter inputs (Kalbitz and Kaiser, 2008; Leff et al., 2012; Tanner et al., 2016; Xu et al., 2013). Consequently, differences in soil chemistry might strengthen the effect of doubling litter inputs by enhancing the stabilization of leached litter-derived carbon via sorption and aggregation (Six et al., 2002). This shows that soil mineralogy and precipitation may both influence the rate of litter decomposition and therefore lead to different results in response to litter manipulation experiments at different sites (Reynolds et al., 2018). Additionally, the carbon sequestration capacity of tropical soils is not well known but plays an important role when estimating if these soils act as carbon sinks or sources in the future (Xu et al., 2013). The capacity of soils to store additional carbon has an upper limit, which is determined by soil chemical, physical and biological factors. Once the limit is reached, soils will not sequester any additional carbon despite the amount of inputs (Six et al., 2002; Xu et al., 2013).

All the factors just mentioned as plot size, climatic conditions, soil mineralogy and carbon sequestration capacity may all also contribute to the highly variable results found in studies held across the globe. Despite these factors, there are two more important drivers for different results across sites and the small increase I found in litter manipulation experiments: priming effects and the origin of soil organic carbon. These two factors are explained in the following chapters.

4.2.2. … because of priming effects

The priming effect happens when easily decomposable, fresh organic material is added to the soil. The additional inputs enhance microbial activity, resulting in the extra decomposition of relatively stable and protected soil organic matter and a disproportionate increase in soil CO_2 efflux (Sayer et al., 2011; Weil and Brady, 2017). This could mean that more carbon is lost from the soil to the atmosphere with doubled litter inputs, resulting in smaller or no net gains. A study conducted at the experimental site in Panama measured soil CO_2 efflux monthly and found significantly higher annual soil respiration and higher CO_2 efflux from soil organic carbon in the double litter treatments compared to the controls (Sayer et al., 2011). Using natural abundance isotopes ($\delta^{13}C$) to track changes in soil organic matter decomposition and cycling, Sayer et al., (2011) showed that 13% of total below-ground respiration is released through priming and this could partially offset predicted net gains in carbon storage. Moreover, it is assumed that the gained soil organic carbon from increased litter inputs has short turnover times (Schlesinger and Lichter, 2001). Soil organic carbon released through priming however is considered as ‘old’ or more stable (Fontaine et al., 2004; Heimann and Reichstein, 2008; Sayer et al., 2011). This would mean that not only is soil organic carbon lost from the soil to the atmosphere, but also that relatively stable carbon is replaced with more labile carbon, resulting in reduced stability of soil organic carbon over the long term (Sayer et al., 2011; Sayer et al., unpublished). Therefore, priming effects could explain the small net gains in soil carbon with double litter inputs found in my study. Moreover, as soil organic carbon released through priming is considered as older or more stable, priming effects could also account for the lower soil organic carbon stocks found at 20-30 cm depth (Figure 9), as the isotope analyses of ^{13}C and ^{15}N showed that more decomposed and stable material can be found in the deeper soil layers.

One reason for priming is the mining of soil organic matter for nutrients, especially when litter with low nutrient content is added (Nottingham et al., 2015). Despite the fact that priming effects were found across different ecosystems types, priming might be greater in nitrogen limited forests, due to the mentioned mining for nitrogen (Nottingham et al., 2015; Whitaker et al., 2014). A meta-analysis of studies about plant growth, soil organic matter dynamics and biological N_2 fixation in FACE experiments (FACE = free air carbon dioxide enrichment) confirmed this assumption. The study describes that soil carbon under elevated CO_2 was unaffected in soils with low nitrogen availability due to priming, whereas experiments under higher nitrogen availably showed significant increases in soil organic carbon (de Graaff et al., 2006). Although in tropical soils, the availability of phosphorus (P) is likely to be relatively more important than N, there is evidence that priming effects are constrained by nutrient availability (Nottingham et al. 2012). Hence, the addition of nutrients with the litter at the study site in Panama could have promoted soil carbon release by priming effects. Priming effects can therefore not only explain relatively small net gains in soil organic carbon with doubled litter inputs but also the variability of results found in different litter manipulation experiments across the globe.

4.2.3. … because soil organic carbon might originate rather from roots than shoots

Another explanation for the relatively small net gains in soil organic carbon in my study is the origin of soil organic carbon. Soil organic carbon originates either from roots or from the decomposition of litter. Roots contribute to the soil organic carbon pool via decomposition of dead root biomass or via releasing organic substances by roots and mycorrhiza, a process called rhizodeposition (Hirte et al., 2018; Rasse et al., 2005). It is nowadays commonly accepted that roots contribute a major part to soil organic carbon stocks, and some scientist suggest that root carbon inputs might even have the biggest impact on carbon sequestration in soils (Brant et al., 2006; Rasse et al., 2005; Schmidt et al., 2011; Sokol et al., 2018). Carbon from litter mostly reaches the mineral soil as dissolved organic carbon but is often considered as labile and therefore only has a short mean residence time in the soil. Consequently, it is often neglected in terms of carbon accumulation in soils (Kalbitz and Kaiser, 2008; Sokol et al., 2018).

In my study, the mass of fine root that was measured during sieving did not change significantly between the double litter and the control treatment. This is also supported by root growth studies at the study site, which found a shift in root growth, with double litter plots showing more roots in the litter layer, but fewer roots in the mineral soil. Overall, there were no changes in root growth between the two treatments (Sayer et al., 2006; Rodtassana & Tanner, 2018). However, soil organic carbon concentrations in my study were correlated with the mass of fine roots (see Chapter 3.1.1 and Figure 8). This indicates that soil organic carbon in the soil originates at least partly from root exudates via rhizodeposition, and hence changes in root biomass, rather than litter inputs, may have a greater effect on soil organic carbon storage. In this case, it is also important to mention that fresh root inputs can stimulate priming effects and therefore boost decomposition and the loss of soil organic carbon, as some root exudates consist of easily decomposable material (Fontaine et al., 2004, 2007). Moreover, the changes I found in soil organic carbon are small compared to the fast turnover time in tropical forests. At the site, normal turnover of organic matter at 0-10 cm depth is 25% in 6 months (Tanner et al., 2016). Consequently, given the rapid turnover of organic matter and the lack of changes in root biomass, it is likely that soil organic carbon originates predominantly from root products rather than leaf litter, explaining the relatively small increase in soil organic carbon found in the experiment (Rasse et al., 2005; Schmidt et al., 2011; Sokol et al., 2018; Tanner et al., 2016).

4.3. Strength and depth effects of litter manipulation do not increase with time

It is likely that the strength and depth of the effects of doubling litter inputs will increase with time. Comparing data from 2007 and 2009, Tanner et al (2016) already found that the effect increased in depth with time for nitrate and phosphorus, leading them to the assumption that strength and depth effects of litter manipulation will increase with time. A stronger effect on total soil organic carbon with time was also proposed in a global meta-analysis of litter manipulation studies by Xu et al. (2013), even though they found no significant effect of experiment duration on the changes in soil organic carbon with additional litter inputs across different biomes. However, litter decomposition rates and mean residence times of soil organic carbon vary widely across ecosystems and therefore make it hard to discover the effect of experiment duration when comparing studies in different ecosystems (Xu et al., 2013). Mean residence times of surface litter in tropical soils are much shorter than in temperate forests with 0.25 to 1 year compared to 4 to 16 years and therefore tropical soils are more sensitive to changes in litter inputs (Olson, 1963; Xu et al., 2013). Despite this, I did not find any evidence that the effects of doubling litter input on soil organic carbon in a tropical forest will be stronger over time. Increases in soil organic carbon concentrations were in the same range over a fifteen-year period of litter manipulation. Measurements after 6 and 13 years showed an increase of 14% and11%, respectively (Tanner et al., 2016; Sayer et al., unpublished), whereas I found a 16.8% increase after 15 years . Moreover, none of the measurements showed a statistically significant difference between double litter and control plots. Indeed, I compared the soil organic carbon concentrations I measured from samples taken in 2018 with measurements done in 2008 and found no statistically relevant differences. The same was true for the calculated soil organic carbon stocks in 2008 and 2018. We can, therefore, assume that there is no clear linear relationship between experimental duration and changes in soil organic carbon with litter addition in tropical soils. This might be also true for other ecosystems as long as the duration of the experiment is longer than the mean residence time of surface litter.

4.4. Limitations of the experiment

The experiment in Panama is long term and large scale and should therefore represent ecosystem scale processes as well as possible for a manipulative experiment. Nevertheless, there are still some limitations and assumptions that limit the broader applicability of the results. It is widely demonstrated that rising

CO_2 concentrations in the atmosphere has increased aboveground NPP in tropical forests and will further increase in the future (Lewis et al., 2009; Pan et al., 2011; Sayer et al., 2011). But no studies state by how much NPP, and consequently litterfall, will increase in the tropics. In the temperate zone, measured increases in litterfall following elevated CO_2 concentration varied amongst experiments and vegetation under survey. A free air CO_2 enrichment (FACE) experiment in a pine plantation showed a 12% increase in litterfall, while another experiment conducted at the Aspen FACE experiment near Wisconsin (US) reported increases in litterfall of 31.3% in the aspen community and 37.6% in the birch-aspen community (Lichter et al., 2008; Liu et al., 2005). It can therefore be assumed that the increase in litterfall due to increased CO_2 in the future will be less than the doubling of litterfall simulated in the experiment (Tanner et al., 2016). This would mean that the already small increases found in soil organic carbon concentrations might be overestimated.

Another important factor influencing the results of the experiment is the litter quality. Doubling litter inputs with ambient litter assumes that litter produced under present atmospheric CO_2 concentrations would have the same effects on soil organic carbon as litter produced under elevated CO_2. However, there is little consensus regarding the changes in litter quality under elevated CO_2 concentration. Kuzyakov (2011) states that litter produced under increased CO_2 concentrations is generally lower quality, meaning that decomposition will be slower due to the higher content of structural materials such as cellulose and lignin. Lower litter quality would counterbalance higher microbial activity linked to priming effects, which in turn might prevent the decomposition of older soil organic carbon in the mineral soil (Kuzyakov, 2011). However, free air CO_2 experiments often show that the C:N ratio of plant tissue, which is a good approximation of litter quality, is not affected by the enrichment in atmospheric CO_2 concentration (de Graaff et al., 2006). If this is also true for the tropics, experiments which double litter inputs with present litter are a realistic approximation in terms of litter quality.

Besides the influence of rising atmospheric CO_2 concentration on litter quantity and quality, which are both considered in litter manipulation experiments, elevated CO_2 concentrations in the atmosphere also have an impact belowground. This frequently called hidden half is neglected when adding litter only aboveground (Kuzyakov, 2011). Previous research has shown that increased CO_2 concentrations did not only increase aboveground biomass production and litterfall, but also belowground plant biomass and rhizodeposition. The effect of elevated CO_2 is even considered to be stronger belowground than aboveground (de Graaff et al., 2006; Kuzyakov, 2011). As we have seen above, more soil organic carbon originates from root biomass and rhizodeposition than from leaf litter. Therefore, impacts of increased atmospheric CO_2 concentrations on belowground production and organic substances released by roots are important and can have different effects on soil carbon sequestration. They should be considered when evaluating if soils will act as carbon sinks or sources in future atmospheric conditions.

5. Conclusion

Continuous doubling of litter inputs over 15 years resulted in a surprisingly minor increase in soil organic carbon stocks over 30 cm depth, which was not statistically significant. The biggest effect was seen at 0-10 cm depth, where there was a trend towards increased soil organic carbon concentrations (16.8%) in the double-litter plots. Nevertheless, the increase in soil organic carbon concentration is smaller than expected. A direct relationship between litter inputs and soil organic carbon would suggest a much greater increase of soil organic carbon. The small increase can be explained by the efflux of carbon through priming and the origin of carbon, where root inputs may be more important than leaf litter. To answer the research questions posed in this master's thesis:

Does doubling litter inputs in a tropical forest increase carbon storage in soil?

Carbon storage increased with doubled litter inputs. However, the increases were minor and not significant.

Which depth increments are most affected by altering litter inputs?

The biggest difference was seen at 0-10 cm depth. The difference between double litter and control plots decreased with depth.

Although the increase in soil carbon stocks was lower than expected, there was still a minor increase in soil carbon in the upper 10-cm due to doubling litter inputs. This increase could partially offset increasing atmospheric CO_2 concentrations. However, the effect of mitigation is very small compared with fossil fuel emissions. Carbon stocks to 30 cm increased by 6.3% over 15 years. On a global scale, around 207 Pg of carbon are stored in the upper 30-cm of tropical soils (Batjes, 1996). An increase of 6.3% would account for an additional 13 Pg stored in tropical soils with doubled litter inputs. By comparison, fossil fuel emissions in 2010 were 8.7 Pg carbon per year (Grace et al., 2014). Over a fifteen-year period, this would mean an increase of 130.5 Pg of carbon in the atmosphere, compared to the additional 13 Pg stored in soils. Moreover, results of increased carbon storage may be overestimated, as the increase in litterfall due to rising atmospheric CO_2 concentrations will be less than the experimental doubling.

In the absence of significant changes of soil organic carbon content between double litter and control plots, the data suggest only a limited potential for this soil to sequester carbon over the long-term in response to rising atmospheric CO_2 concentrations. Still, litter manipulation experiments provide valuable information for the estimation of how litter affects soil organic carbon formation and cycling. However, the current lack of long-term experiments in the tropics makes it difficult to estimate the carbon sequestration capacity of tropical soils. Moreover, altered litter production caused by environmental changes could lead to cascading effects on other soil properties, which in turn would influence carbon dynamics and rising atmospheric CO_2 concentrations do not only alter aboveground NPP but also other factors regulating carbon cycling in soils (Xu et al., 2013).

With that many challenges and our currently lacking understanding of carbon dynamics, we cannot predict if tropical soils will act as a source or sink of carbon in a future environment. But they highlight the importance of more research and results from litter manipulation experiments. A better understanding of soil carbon storage and cycling in tropical soils as well as of plant-soil feedbacks would improve predictive models of changes in global carbon stocks because such models often assume a direct relationship between litter and soil carbon. The results of this master's thesis show that this assumption is incorrect and that there is no direct relationship. Moreover, it highlights the importance of plant-soil feedbacks for predictions of the carbon sequestration potential of tropical soils in future climatic conditions. Including these mechanisms will not only improve models but will also allow greater preparedness for the consequences of climate change.

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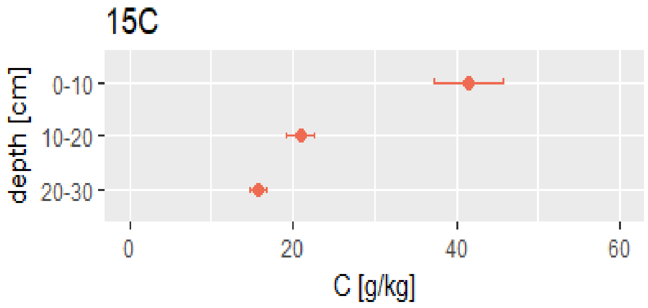
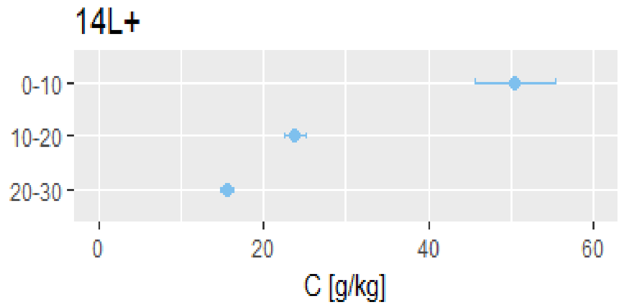
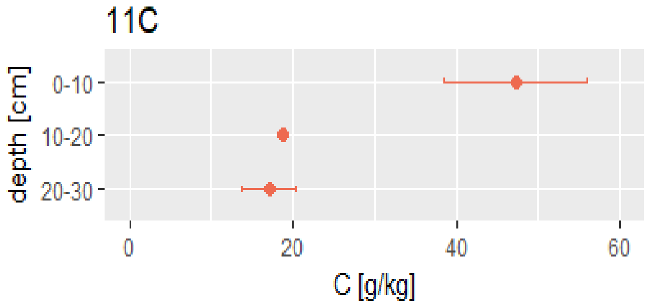
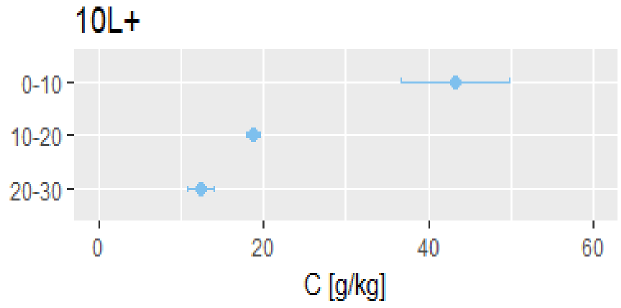
Appendix

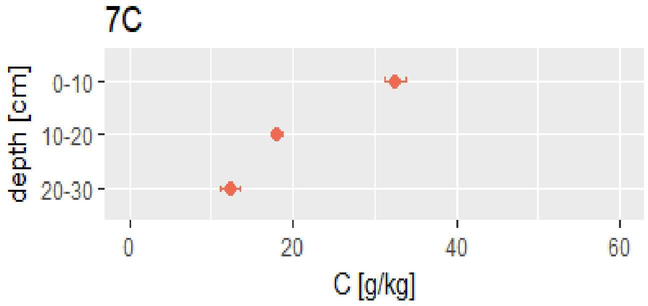
A. Soil organic carbon values per plot and depth

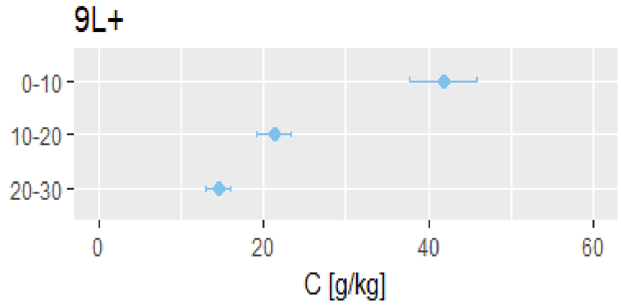


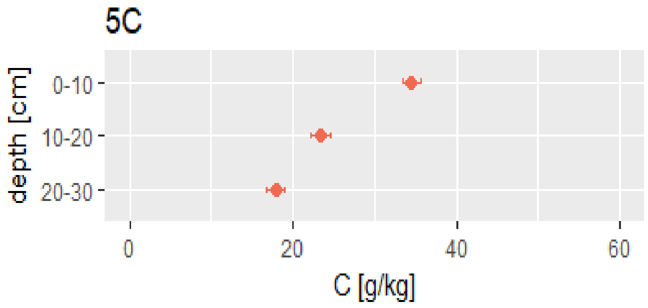


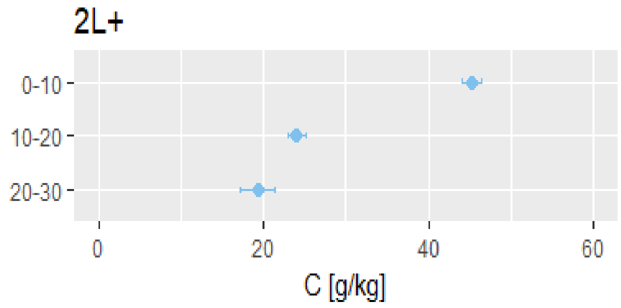


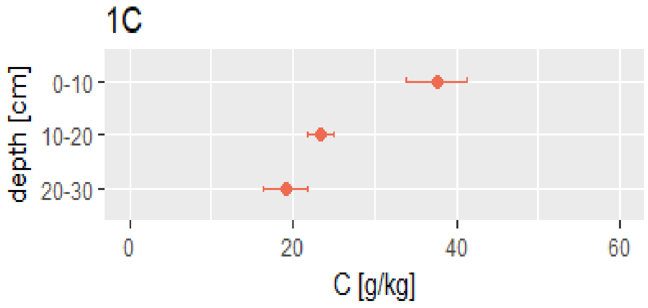


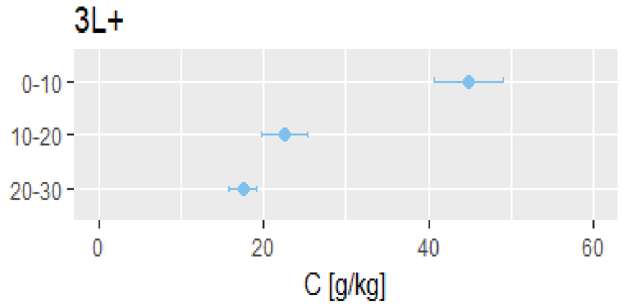












B. Data

Plot Number	Depth (cm)	mean C (%)	SE C	mean N (%)	SE N	delta C (‰)	delta N (‰)	bulk density (g/cm^3)	Stock (t/ha)
15C	0-10	4.14	0.73	0.39	0.04	-27.79	6.38	0.59	24.51
	10-20	2.09	0.30	0.20	0.05	-26.65	6.45	0.86	18.02
	20-30	1.57	0.17	0.14	0.02	-26.47	6.45	1.06	16.70
14L+	0-10	5.05	0.85	0.46	0.07	-27.72	6.32	0.56	28.42
	10-20	2.38	0.23	0.23	0.02	-26.63	6.41	0.86	20.49
	20-30	1.56	0.13	0.14	0.00	-26.05	6.38	1.06	16.61
11C	0-10	4.72	1.52	0.43	0.12	-28.03	6.23	0.55	25.77
	10-20	1.87	0.10	0.17	0.01	-26.22	6.24	0.86	16.09
	20-30	1.71	0.58	0.16	0.05	-25.75	6.19	1.06	18.21
10L+	0-10	4.33	1.13	0.32	0.07	-27.88	6.08	0.47	20.52
	10-20	1.87	0.14	0.16	0.01	-26.55	6.14	0.86	16.10
	20-30	1.24	0.26	0.11	0.02	-25.90	6.08	1.06	13.24
9L+	0-10	4.18	0.71	0.39	0.06	-27.85	5.98	0.66	27.46
	10-20	2.13	0.37	0.21	0.03	-26.64	6.04	0.86	18.33
	20-30	1.45	0.27	0.14	0.01	-25.87	6.00	1.06	15.47
7C	0-10	3.25	0.23	0.30	0.01	-27.49	5.83	0.54	17.70
	10-20	1.80	0.12	0.17	0.02	-26.15	5.90	0.86	15.46
	20-30	1.23	0.20	0.12	0.02	-24.60	5.94	1.06	13.12
5C	0-10	3.45	0.19	0.30	0.02	-27.29	5.70	0.56	19.27
	10-20	2.34	0.22	0.20	0.02	-26.53	5.75	0.86	20.17
	20-30	1.79	0.20	0.15	0.02	-26.02	5.78	1.06	19.02
3L+	0-10	4.49	0.73	0.39	0.03	-28.12	5.60	0.54	24.08
	10-20	2.26	0.49	0.20	0.05	-26.55	5.66	0.86	19.43
	20-30	1.75	0.29	0.16	0.02	-25.97	5.70	1.06	18.67
2L+	0-10	4.52	0.20	0.40	0.02	-27.66	5.60	0.53	23.84
	10-20	2.40	0.18	0.21	0.01	-26.44	5.71	0.86	20.61
	20-30	1.93	0.36	0.17	0.03	-25.89	5.75	1.06	20.57
1C	0-10	3.76	0.65	0.34	0.05	-27.54	5.70	0.57	21.43
	10-20	2.33	0.28	0.22	0.05	-26.39	5.73	0.86	20.08
	20-30	1.91	0.47	0.17	0.05	-25.65	5.76	1.06	20.30

Personal declaration:
I hereby declare that the submitted thesis is the result of my own, independent work. All external sources are explicitly acknowledged in the thesis.

Zurich, September 2019

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