DROUGHT EFFECTS ON SOIL CARBON DIOXIDE EFFLUX IN TWO ECOSYSTEMS IN CENTRAL SULAWESI, INDONESIA

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"Humankind has not woven the web of life. We are but one thread within it. Whatever we do to the web, we do to ourselves. All things are bound together. All things connect.

- Chief Seattle, 1854 -

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Summary

Drought response on soil CO_2 efflux and production dynamics were examined in two tropical ecosystems in central Sulawesi, Indonesia. Large-scale throughfall displacement roofs were built in a cacao (*Theobroma cacao*) / *Gliricidia sepium* agroforestry plantation (560 m.a.s.l.) and in an undisturbed sub-montane tropical rainforest (1,050 m.a.s.l.) to simulate drought conditions. At each site, ecosystem drought responses from three roof plots were compared to three undisturbed control plots. Soil CO_2 production was measured spatially at the soil surface and vertically within the soil profile to 2.5 m depth every two weeks.

1. The simulated drought in the cacao / *Gliricidia* agroforestry ecosystem consisted of a one month baseline evaluation phase, a 13 months simulated drought and a five months rewetting phase. During the drought phase of the experiment soil CO_2 efflux decreased by 13% in comparison to the control. The mild drought response is attributed to two reasons. First, soil CO_2 efflux peaked at intermediate soil moisture contents, but was low when soil conditions became dry (in the induced drought plots) and when the soil became very wet (in the control plots). This means that respiration differences between control and roof plots may have been masked when soil moisture conditions were wet in the control and concurrently very dry in roof plots. Secondly, CO_2 efflux drought response was localized. At some measurement chamber sites (n = 11) drought effects were very pronounced: soil CO_2 efflux decreased as soil moisture levels decreased. At other chamber sites (n = 7) however, there was no evident drought effect on soil CO_2 emissions. Soil CO_2 efflux was highest at the base of tree stems and decreased with distance radiating outwards. Overall, the experiment had a CO_2 neutral effect: the decreases in emissions during the induced drought period were compensated for during the five month rewetting phase when CO_2 efflux rebounded and surpassed the control.

2. The simulated drought in the undisturbed sub-montane tropical rainforest consisted of a two and a half months baseline evaluation phase, a 24.5 months simulated drought and a four months rewetting phase. In contrast to the cacao agroforest, the sub-montane tropical rainforest experienced a severe decrease in soil CO_2 production. Here, soil CO_2 efflux decreased by an average of 39 % in comparison to the control during the induced drought period. Soil moisture, the main variable controlling CO_2, exhibited a strong positive linear relationship with soil CO_2 production ($R^2 = 0.72$). A two phase ecosystem drought response was observed. During the first phase, which lasted nine months, leaf litter respiration declined

as did the CO_2 production between 30 and 70 cm soil depth. During the second phase of the experiment (the next 16 months) drought conditions intensified further and belowground CO_2 production from heterotrophic and autotrophic sources decreased at all soil depths. Leaf litter respiration remained negligible. Recuperation after the drought was slow in this ecosystem and did not rebound to control plot levels. In this ecosystem, the simulated drought resulted in a reduction in overall CO_2 emission.

Zusammenfassung

Zur Untersuchung des Einflusses von Trockenheitsperioden auf die unterirdische Kohlenstoffdynamik wurden Emissions- und Produktionsraten von CO_2 in den Böden zweier tropischer Ökosysteme in Zentralsulawesi/Indonesien gemessen. Für diese Untersuchungen wurde eine künstliche Trockenheit mit Hilfe von Dächern aus durchsichtiger Folie erzeugt, die den Bestandesniederschlag von drei Versuchsflächen im Vergleich zu drei Kontrollflächen verringerten. Ein solches Trockenheitssimulationsexperiment wurde in einem Kakao (*Theobroma cacao*) / *Gliricidia sepium* Agroforst (560 m ü.NHN) durchgeführt, und ein weiters in einem sub-montanen tropischen Regenwald (1,050 m ü.NHN). Alle zwei Wochen wurde die Produktion von CO_2 sowohl horizontal-räumlich als auch vertikal bis zu einer Tiefe von 2,5 m gemessen. Die CO_2-Produktion der bedachten Flächen wurde dabei mit den Kontrollflächen verglichen.

Das Simulationsexperiment im Kakao / *Gliricidia* Agroforst bestand aus einer einmonatigen Vorphase (vor der künstlichen Austrocknung), gefolgt von einer 13 monatigen Trockenheitssimulation und einer fünfmonatigen Wiederbefeuchtungsphase. Während der Trockenphase war die CO_2-Emission aus dem Boden im Vergleich zu den Kontrollflächen um 13 % reduziert. Diese relativ schwache Reaktion kann auf zweierlei Weise erklärt werden. Die Emission von CO_2 in den Dach- wie auch in den Kontrollflächen war bei mittlerer Bodenfeuchtigkeit am höchsten, und sehr niedrig wenn die Bodenfeuchte entweder sehr gering oder sehr hoch war. Daher konnten kaum Unterschiede in der Bodenrespirationsrate zwischen Kontrollflächen und Dachflächen festgestellt werden, wenn die Bodenfeuchtigkeit in den Kontrollflächen hoch war, während die Dachflächen gleichzeitig sehr trocken waren.

Weiterhin zeigten die von der simulierten Trockenheit beeinflussten CO_2-Emissionen in den Dachflächen eine starke räumliche Variabilität. An einigen Messpunkten (n = 11) war der Einfluss der simulierten Trockenheit sehr deutlich. Die CO_2-Emissionen nahmen hier mit verminderter Bodenfeuchtigkeit ab. An anderen Messpunkten (n = 7) konnte dagegen kein Einfluss der Bodenfeuchte auf die CO_2-Emissionen festgestellt werden. Die CO_2-Emissionen des Bodens waren am höchsten am Fuß der Bäume und nahmen mit zunehmender Entfernung von diesen ab. Insgesamt glichen sich die CO_2-Emissionen von Dach- und Kontrollflächen über die Zeitdauer des Experimentes aus: Die Emissionen auf den Dachflächen waren während der simulierten Trockenheit niedrig, nahmen aber während der fünfmonatigen Wiederbefeuchtungsphase zu, wobei sie sogar die Emissionen der Kontrollflächen übertrafen.

In einem weiteren Trockenheitsexperiment wurde die unterirdische Kohlenstoffdynamik eines tropischen Regenwaldes untersucht. Das Simulationsexperiment begann mit einer zweieinhalbmonatigen Vorphase (vor der künstlichen Austrocknung), gefolgt von einer 24,5-monatigen Trockenheitssimulation und einer viermonatigen Wiederbefeuchtungsphase. Im Gegensatz zu dem Experiment im Kakao / *Gliricidia* Agroforst war die CO_2-Produktion im Regenwald bei Trockenheit stark vermindert. Die CO_2-Emissionen in den Dachflächen nahmen im Vergleich zu den Kontrollflächen um durchschnittlich 39 % ab. Die Bodenfeuchtigkeit, die Haupteinflussgröße der CO_2-Produktion, war stark lineare positiv mit der CO_2-Produktion korreliert ($R^2 = 0.72$). Die Reaktion auf die simulierte Trockenheit verlief in zwei Teilen: In den ersten neun Monaten nahm die Respirationsrate der Laubstreu ab, die autotrophe (Wurzeln) und die heterotrophe Respiration (Mikroorganismen) im Boden blieb indes unverändert. Die CO_2-Produktion in den oberen Bodenschichten nahm dabei zu, während sie in tieferen Schichten abnahm. Während der nächsten 16 Monate des Experiments verstärkte sich die Auswirkung der Trockenheit und die autotrophe und heterotrophe CO_2-Produktion nahm in allen Bodentiefen ab. Die Respirationsrate der Laubstreu blieb dabei sehr gering. Während der Wiederbefeuchtungsphase stiegen die CO_2-Emissionen in den Dachflächen an. Die Emissionswerte der Kontrollflächen wurden dabei allerdings nicht mehr erreicht. Im Ökosystem Regenwald führte eine Trockenheit daher zu insgesamt verminderten CO_2-Emissionen.

CHAPTER 1

INTRODUCTION

1   Climate change and the carbon cycle

Since the beginning of the industrial revolution, atmospheric carbon dioxide (CO_2) concentrations have been increasing exponentially as a result of anthropogenic CO_2 emissions from fossil fuel burning, deforestation, land clearing and fire. Higher concentrations of CO_2 and other greenhouse gasses in the atmosphere are causing an imbalance between incoming solar radiation and outgoing infrared radiation (Forster *et al.*, 2007). The increased radiative forcing is causing global temperatures to rise. As a result, global and regional climate patterns are changing. The effects of global warming (rising temperatures, changing circulation patterns, rising sea levels, melting ice caps and higher frequencies of extreme weather events such as droughts, severe storms, and flooding) will have severe impacts on ecosystems worldwide and will affect the livelihoods of millions of people (IPCC, 2007).

Anthropogenic carbon dioxide emissions attributed to the global warming remain small however in comparison to natural sources coming from oceans and the terrestrial biosphere. The circulation of carbon through the atmosphere with the terrestrial biosphere, the ocean biosphere and the Earth's crust is known as the global carbon cycle (Fig. 1).

As illustrated in Figure 1, the global carbon pools contain 39,000 petagram carbon ($Pg = 10^{15}$ g) in oceanic pools, 6,000 Pg C bound in fossil fuels, 3,150 Pg stored as soil carbon, 750 Pg in atmospheric carbon, and 650 Pg C stored in vegetation (Sabine *et al.*, 2004). Soil carbon stocks alone contain four times more carbon than is stored in the atmospheric pool and nearly five times that in vegetation pool. The carbon pools are interconnected with each other and circulate carbon from one pool to the other. The exchanges of carbon between pools are called fluxes. In the terrestrial carbon cycle, 121 Pg C per year are taken up from the atmospheric pool through photosynthesis, 44 Pg C yr^{-1} is returned to the atmosphere through aboveground plant respiration and 75 Pg C yr^{-1} by soil respiration (Luo and Zhou, 2006).

Prior to human manipulation of the carbon cycle, upward fluxes (emissions) into the atmosphere from natural sources were almost equally offset by transfers back into other carbon reservoirs (Schlesinger *et al.*, 2000). The imbalance created by man-made carbon dioxide emissions illustrates that even slight changes in atmospheric CO_2 concentrations will have severe consequences on global climate change. Global warming induced changes in terrestrial ecosystem functions and specifically in carbon allocations and stocks can therefore have potentially severe consequences on return fluxes to the atmosphere (Heimann and Reichstein, 2008).
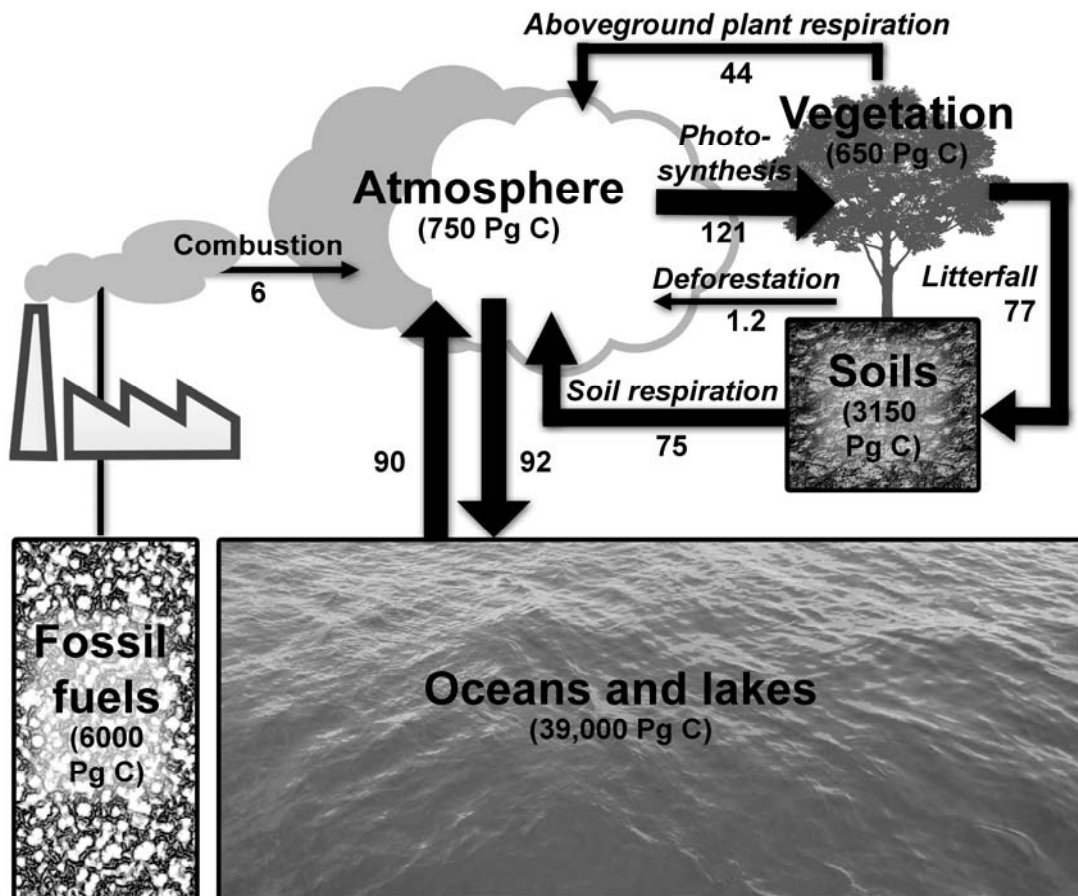
Figure 1: A simplified version of the global carbon cycle highlighting the carbon pools and fluxes associated with the atmosphere, the terrestrial biosphere and the oceans. The pools are expressed in Petagram (Pg $=10^{15}$ g) and fluxes, indicated using arrows are in Pg yr^{-1} (Adapted from Brady and Weil (1999)).

Carbon dioxide concentrations and fluxes in the global carbon cycle have major influences on the dynamics of the global climate: on the hydrosphere, the atmosphere, the biosphere and on the pedosphere. While many studies have focused on the atmospheric and hydrospheric changes as well as on the impacts of climate change on the biosphere, very little emphasis has been given to soil carbon dynamics, especially in tropical environments.

2   Soil respiration

In the terrestrial environment, photosynthetic processes fix atmospheric carbon dioxide and convert CO_2 to organic carbon compounds. Some of the carbon compounds produced are utilized by plants as an energy source, which in the process release CO_2 back to the atmosphere. This is called plant respiration. Moreover, plants use carbon compounds to grow new leaves, roots, and wood. While leaves and roots may store carbon for a few months or years, wood can potentially retain carbon for decades or even centuries. Eventually however,

when the organic matter dies it is decomposed by microorganisms, which in the process releases CO_2 back into the atmosphere. This is referred to as heterotrophic respiration. Accumulated organic residues from dead plants and microbial biomass make up soil organic matter (SOM). The carbon stored in SOM can persist in the soil for hundreds to thousands of years before eventually being broken down. Respiration from roots is called belowground autotrophic respiration. Soil respiration, also referred to as CO_2 efflux, is a combination of both heterotrophic and belowground autotrophic sources (Luo and Zhou, 2006).

Respiration is a biochemical process of living organisms (plants, micro-organisms, and animals), and the rate and quantity of CO_2 produced through this process is determined by biological productivity of organisms and the environmental variables that affect them. Both soil temperature and soil moisture are regarded as the primarily controlling variables that influence soil respiration (Davidson *et al.*, 2000, Raich and Schlesinger, 1992, Risk *et al.*, 2002). Additionally however, soil pH, soil texture, soil aeration and soil fertility are also important factors (Luo and Zhou, 2006).

3   Drought effects on tropical ecosystems

The complex chain of reactions caused by global temperature rises will also affect regional hydrological cycles (Bates *et al.*, 2008). Anticipated increases in temperatures, combined with decreased precipitation, will enhance evapotranspiration and decrease soil moisture. Consequently, drought occurrence will become more common in many regions of the world. In the tropics, droughts have been linked to changes in sea surface temperatures, which through associated changes in atmospheric circulation patterns affects regional precipitation (Bates *et al.*, 2008). The periodic El Niño Southern Oscillation (ENSO) phenomenon is one such anomaly, which historically has been shown to cause droughts. Quinn *et al.* (1978) for example, found that the ENSO phenomenon were associated with 93% of droughts experienced in Indonesia between 1830 and 1953. Recent research indicates that climatic changes will increase the frequency of the ENSO phenomenon (Timmermann *et al.*, 1999). Climate change prediction models also anticipate regional increases in drought occurrence and intensity across the tropics (Cox *et al.*, 2004, Sheffield and Wood, 2008).

Droughts will not only have potentially dire consequences on food production and human livelihoods, but it will also have direct effects on the global and regional carbon cycles. Drought induced carbon flux changes can take a number of forms including: increased fires (Page *et al.*, 2002), increased vegetation mortality (Clark, 2004, Van Nieuwstadt and Sheil,

2005, Williamson *et al.*, 2000) and changes in biomass partitioning (Brando *et al.*, 2008, Nepstad *et al.*, 1994). Severe water deficits in plants can among other effects cause catastrophic xylem embolisms, cell dehydration, reduce leaf size, and carbon starvation due to stomata closure (Farooq *et al.*, 2009). Indirectly, stressed ecosystem also become increasingly vulnerability to insects and diseases (McDowell *et al.*, 2008). The extent of drought stress will depend on the mechanisms available to withstand the drier conditions. Plant adaptations and acclimations to these stresses include deep and prolific root systems, osmotic adjustment, increased diffusive resistance, and development of small and succulent leaves (Farooq *et al.*, 2009).

Droughts will not only have aboveground effects but will also have direct and indirect consequences on soil surface and belowground biological processes. Soil moisture changes are known to affect microbial activity, root growth and turnover, decomposition processes, leaf litterfall and aboveground biomass productivity (Davidson *et al.*, 2008). The conceptual diagram of soil CO_2 production and transport, shown in Figure 2, is a modification of the model developed by Fang and Montcrieff (1999). The diagram demonstrates how CO_2 production from roots and microbial respiration is influenced by environmental conditions (temperature, soil moisture, and soil oxygen). The rate and quantity of CO_2 respired at the soil surface is a function of gas diffusivity, which is regulated by soil water contents, soil physical properties and temperature (de Jong and Schappert, 1972). In the event of a drought, both altered soil physical conditions (less water in the soil profile), and vegetation drought responses (changes in litterfall, carbohydrate transfers, root activity and root mortality), will consequently affect belowground CO_2 production and emission dynamics.

Tropical soils are estimated to contain nearly one third of the global soil carbon stock (approximately 692 Pg C) (excluding permafrost soils and wetlands) (Jobbágy and Jackson, 2000). Therefore, given the natural short residence times of carbon in tropical soil and the higher than average CO_2 production, carbon pools in the tropics may be particularly vulnerable to changing soil moisture regimes due to drought (Amundson, 2001, Trumbore, 2006). The increased frequency of severe weather events already observed in recent history, as well as the fact that tropical soils store large amounts of carbon, remind us that a better understanding of soil carbon dynamics in tropical soils in a changing climate is of utmost importance to better predicting future carbon fluxes to the atmosphere.
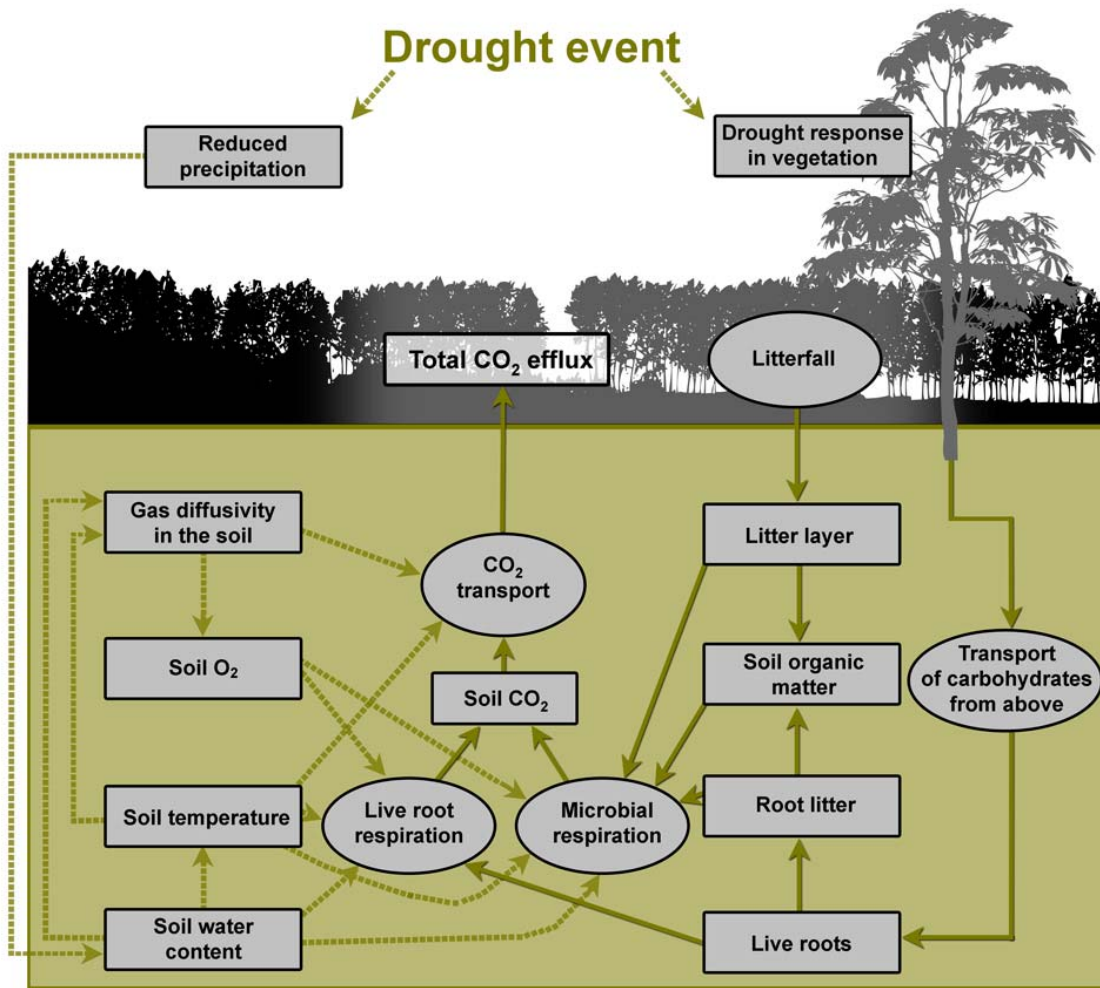
Figure 2: Soil CO$_2$ efflux processes. A conceptual diagram describing drought event influences on soil surface and belowground soil CO$_2$ efflux processes (Modified from Fang and Montcrieff (1999)). Rectangles indicated state variables, ellipses indicate processes; solid lines indicate carbon flows, while dashed lines indicate the influence of environmental conditions on gas transport.

4   Project objectives and justifications

In comparison to aboveground biomass estimations, relatively little is known on belowground carbon dynamics despite the fact that they contain five times more carbon. The research undertaken in this dissertation attempts to understand the fate of belowground carbon and the return fluxes to the atmosphere during and after a drought in Sulawesi. We focused on two ecosystems, one in an undisturbed sub-montane tropical forest and a second in a cacao (*Theobroma cacao*) and *Gliricidia sepium* agroforestry system. These two ecosystems were selected because of their regional importance to understanding carbon dynamics and, in the case of cacao, because of its rapidly expanding landuse and tremendous economic importance to small-scale farmers. The focus of this study was to examine how an experimental drought affects soil respiration. Specifically the research objectives were as follows:

1. To characterize the temporal drought effects and ecosystem recuperation on soil respiration and soil CO_2 production.

2. To identify the environmental controls regulating soil CO_2 efflux and production.

3. To partition CO_2 production sources and to identify how they react to drought and rewetting.

4. To identify spatial patterns in soil CO_2 efflux.

5   Experiment design and implementation

The experiment was conducted within the framework of the Stability of Rainforest Margins (STORMA) project, a multidisciplinary research project funded by the German Science Foundation (DFG) which focused on issues of social and ecological sustainability of the Lore Lindu National Park (Fig. 3).
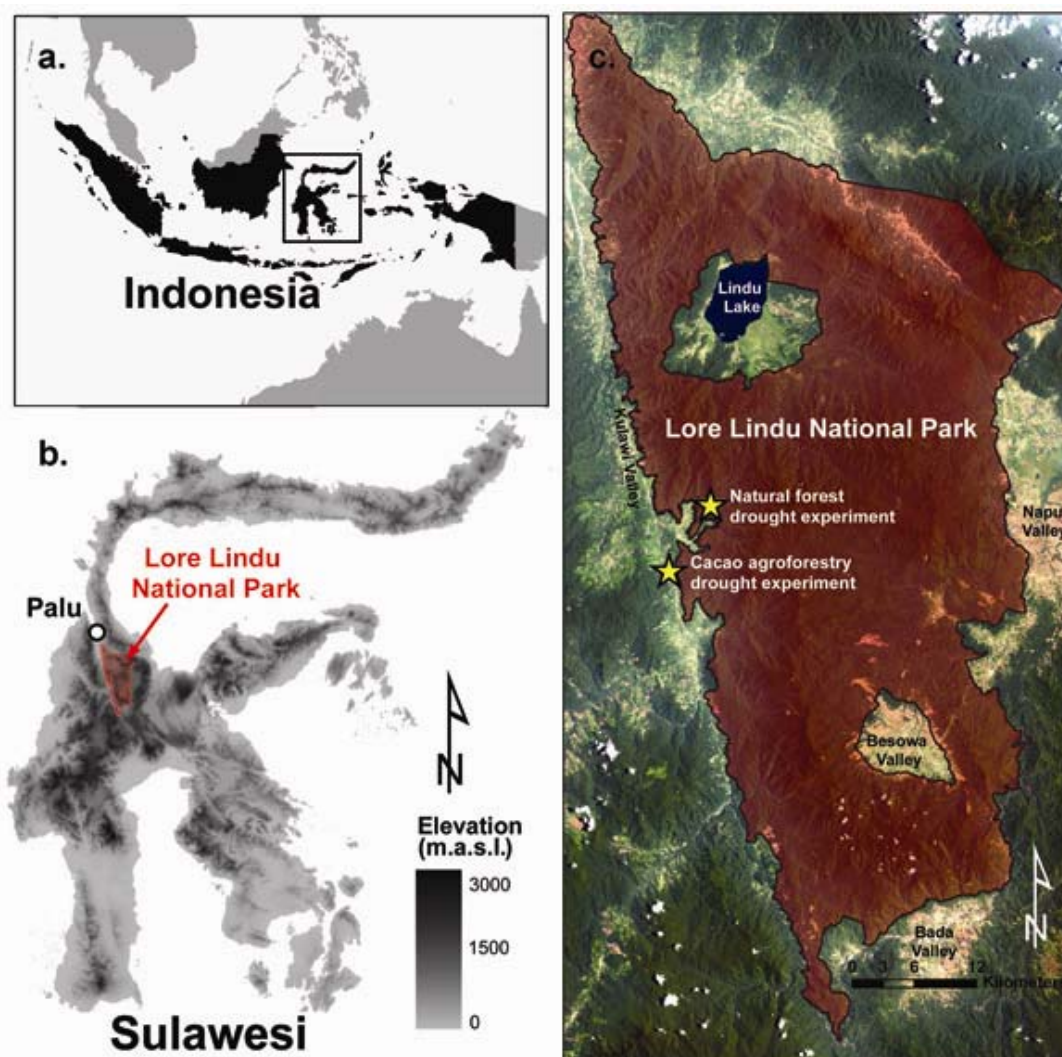
Figure 3: The location of the two drought simulation experiments in (a) Indonesia, (b) Sulawesi, (c) Lore Lindu National Park.

Two drought simulation experiments were conducted at the western edge of the National Park: one in a cacao / *Gliricidia* agroforestry plantation and a second in a natural sub-montane tropical forest. To simulate drought effects, we established large-scale throughfall diversion roofs in both ecosystems. The aim of establishing the roofs was to divert incoming water away from the plot and subsequently dry out the underlying soil. The experiment was set up using a stratified random design experiment, whereby soil respiration under the three roof plots was compared with three adjacent control plots which received normal precipitation (Fig. 4 and 5). The roofs were built in the understory of each ecosystem at a height ranging from 1.2 to 2.0 meters above the ground. Each roof experiment consisted of several thousand individual throughfall diversion panels and a series of gutters through which diverted water flowed through to a location down slope of the plot (Fig. 6a and b). The panels which were long and narrow (0.5 x 5 m) consisted of a bamboo frame onto which transparent plastic was attached.
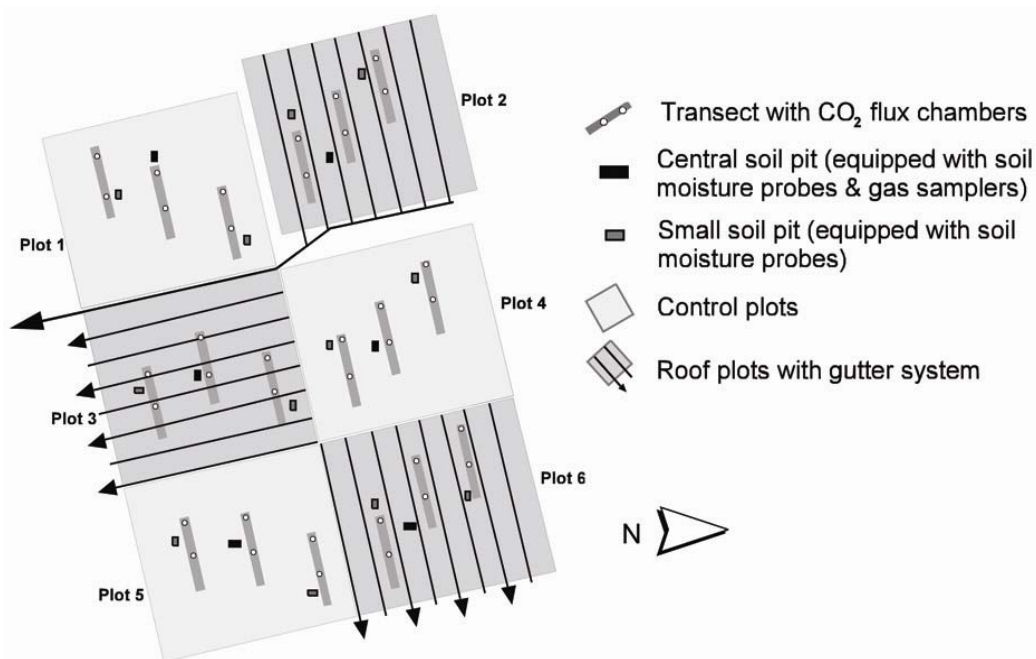
Figure 4: Drought simulation experiment plot layout in the cacao / *Gliricidia* **agroforestry system**

Soil CO_2 dynamics were measured every two weeks spatially across the experimental plots and vertically within the soil profile down to 2.5 meters. Spatial measurements of soil CO_2 efflux were measured at 36 permanently installed measurement chambers spread out across the plots. CO_2 efflux was measured using a portable infrared CO_2 gas analyzer (IRGA). In the soil profile, soil CO_2 production profiles were modeled using soil air CO_2 concentrations from different depths in the soil profile and the respective volumetric water content for each

measurement date in combination with other soil physical properties. The modelling approach utilized was first described by de Jong and Schappert (1972).
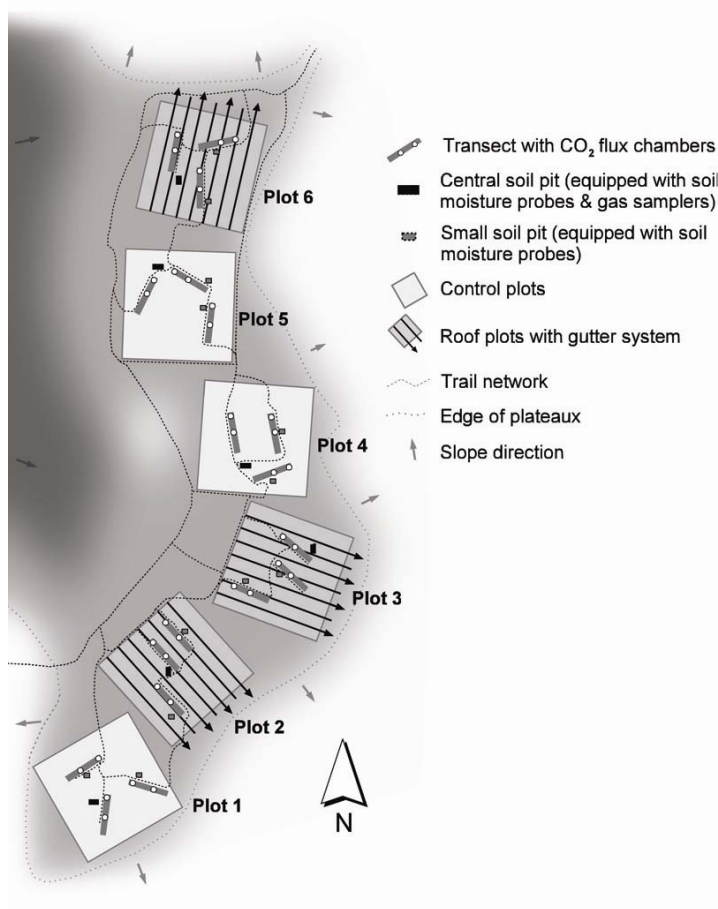
Figure 5: Drought simulation experiment plot layout of the tropical forest site

Furthermore, CO_2 contribution from the leaf litter layer was measured at each site in an additional litter removal / litter doubling experiment. At the forest site, an additional experiment was set up to separate belowground respiration into autotrophic and heterotrophic sources using a root trenching and exclusion design.

Figure 6: Pictures of the throughfall displacement roof in a) the cacao agroforestry site and b) the sub-montane tropical forest site

Further details into the site descriptions and measurement methodologies for each respective site are elaborated on at greater length in the Materials and Methods sections in Chapter 2 for the cacao agroforestry study and Chapter 3 for the natural forest site.

This dissertation constitutes the research from two experiments. Chapter two describes how soil CO_2 efflux in a cacao agroforest ecosystem is affected by a 13 months simulated drought. Chapter three reports on belowground CO_2 production dynamics spatially as well as vertically in a 24.5 month drought simulation experiment conducted in an undisturbed natural forest. Chapter four is a synthesis of the results of the two studies and attempts to extrapolate results to regional and global scales.

CHAPTER 2

SPATIAL AND TEMPORAL EFFECTS OF DROUGHT ON SOIL CO_2 EFFLUX IN A CACAO AGROFORESTRY SYSTEM IN SULAWESI, INDONESIA

Spatial and temporal effects of drought on soil CO_2 efflux in a cacao agroforestry system in Sulawesi, Indonesia

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Abstract

Climate change induced droughts pose a serious threat to ecosystems across the tropics and sub-tropics, particularly to those areas not adapted to natural dry periods. In order to study the vulnerability of cacao (*Theobroma cacao*) - *Gliricidia sepium* agroforestry plantations to droughts a large scale throughfall displacement roof was built in Central Sulawesi, Indonesia. In this 19-month experiment, we measured soil surface CO_2 efflux (soil respiration) in three roof plots compared with three adjacent control plots. Soil respiration rates peaked at intermediate soil moisture and either decreased under increasingly dry conditions (drought induced), or under increasingly wet conditions (as evidenced in control plots). The roof plots exhibited a slight decrease in soil respiration compared to the control plots (average 13 % decrease). The strength of the drought effect was spatially variable – while some measurement chamber sites reacted strongly ("responsive") to the decrease in soil water content (up to $R^2 = 0.70$) (n = 11), others did not react at all ("non-responsive") (n = 7). A significant correlation was measured between 'responsive' soil respiration chamber sites and sap flux density ratios of cacao (R = 0.61) and *Gliricidia* (R = 0.65). Leaf litter CO_2 respiration decreased as conditions became drier. During dry periods the litter layer contributed approximately 3-4 % of the total CO_2 efflux and up to 40 % during wet periods. A CO_2 flush was recorded during the rewetting phase that lasted for approximately two weeks, during which time accumulated labile carbon stocks mineralized. The net effect on soil CO_2 emissions over the duration of the experiment was neutral, control plots respired 11.1 ± 0.5 Mg C ha^{-1} yr^{-1}, while roof plots respired 10.5 ± 0.5 Mg C ha^{-1} yr^{-1}.

1 Introduction

In recent decades, Indonesia has experienced severe droughts that were related to El Niño Southern Oscillation (ENSO) events (Quinn *et al.*, 1978, Sheffield and Wood, 2008). Some climate prediction models suggest that droughts in Indonesia may become more frequent and more severe in the future (Sheffield and Wood, 2008, Timmermann *et al.*, 1999). Changes in precipitation patterns due to climatic change, including droughts, will have direct effects on agricultural productivity (Sivakumar *et al.*, 2005) and the terrestrial biosphere carbon cycle (Tian *et al.*, 2000). Understanding how ecosystems and specifically carbon dynamics respond to droughts is important given the feedback potentials to the atmosphere from carbon dioxide (CO_2) emissions. Decreases in precipitation have been shown to affect plant root dynamics, litter fall, soil organic matter decomposition, nutrient mineralization rates, as well as soil aeration - which in turn affects gas diffusion and microbial processes (Davidson *et al.*, 2004). Exactly how an ecosystem will react to drought conditions is largely dependent on the mechanisms it has available to adapt to droughts. The presence or absence of deep root systems is one such mechanism. Studies carried out in tropical forests of Latin America suggest that ecosystems with deep rooted trees are more capable to mitigate drought effects (Davidson *et al.*, 2004, Nepstad *et al.*, 1994).

Droughts in Indonesia pose a potential threat to both natural forest ecosystems and agricultural production systems such as cacao (*Theobroma cacao*). In the last 25 years, Indonesia has experienced a boom in cocoa production and has since become the third largest producer of cocoa beans worldwide (FAO, 2009). Nearly 80 % of the cocoa beans produced in Indonesia are grown in Sulawesi. It is unknown how well cacao agroforestry plantations are adapted to drought conditions, although a recent socio-economic survey by Keil *et al.* (2008) in central Sulawesi found that cocoa production is vulnerable to drought. Unlike cacao trees which tend to have a shallow rooting architecture (Kummerow *et al.*, 1982), agroforestry over-story trees such as *Gliricidia* (*Gliricidia sepium*) often have deeper root systems.

To date, little has been published on belowground carbon dynamics in agroforestry systems (Bailey *et al.*, 2009, Hergoualc'h *et al.*, 2008, Oelbermann *et al.*, 2006), and as far as we are aware, no soil CO_2 efflux measurements have been carried out in tropical agroforestry systems in relation to drought stress.

In a replicated experiment, we investigated how a cacao – *Gliricidia* agroforestry plantation in central Sulawesi, Indonesia reacted to an experimental drought. In an earlier

paper by Schwendenmann *et al.* (2010) it was shown that this agroforest was surprisingly resilient to drought conditions which was explained by a combination of complementary use of soil water resources and acclimation. Here we report how the experimental drought affected soil CO_2 production and efflux. The specific research objectives for this study were twofold:

1. To determine how belowground carbon dynamics (specifically CO_2 production) reacted to a simulated drought and the subsequent rewetting phase.
2. To identify the controls driving CO_2 efflux.

At the beginning of the experiment we suspected that this agroforestry system would be vulnerable to drought stress and we hypothesized that soil respiration rates will show strong decreases across the plantation with the severity and duration of the drought affecting the degree of the CO_2 drought response. Furthermore, if the drought becomes so severe that there is significant root mortality CO_2 emissions may become more difficult to predict, as a drought-induced reduction in root and heterotrophic respiration may be compensated for by an increase in dead roots which may lead to an increase in decomposition. Finally, during the rewetting phase following the drought we expected a strong increase in CO_2 production in the drought plots.

2   Materials and Methods

2.1 Site description

The drought simulation experiment was conducted in a seven year old cacao agroforestry plantation on the western periphery of the Lore Lindu National Park (1.552°S, 120.020°E) in Central Sulawesi, Indonesia at an elevation of 560 m above sea level (a.s.l.). Established in December 2000, the plantation was composed of a *Gliricidia* (*Gliricidia sepium* (Jacq.) Kunth ex Steud.) overstory (~ 330 trees ha^{-1}) and a cacao (*Theobroma cacao* L) understory ($\sim 1,030$ trees ha^{-1}). The ground was largely devoid of undergrowth herbs and grasses except for a few patches of grass in open areas. We selected a site that was located on a gentle slope (8-12°), where the ground water table (> 4.5 m) was deeper than the tree rooting zone. The region experiences two mild rainy seasons per year. The average annual precipitation at the Gimpu meteorological station (417 m.a.s.l.) five kilometres south of the experimental site was 2092 mm. The mean annual temperature for 2002 - 2006 was 25.5°C (Schwendenmann *et al.*, 2010).

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The soil has been classified as a Cambisol with a sandy loam texture (Leitner and Michalzik, unpublished data). The top 75 cm of soil has a relatively homogeneous texture, a stone content of 15 - 25 % and a bulk density of 1.31 ± 0.06 g cm^{-3}. Below 75 cm the sub-soil is heterogeneous, made up of saprolite, irregular granitic rock fragments embedded in a quartz-feldspar rich loam. The bulk density of the subsoil is 1.56 ± 0.08 g cm^{-3}. Soil chemical and physical properties for the control and roof plot soil profiles are summarized in Table 1.

While the majority of cacao fine roots (diameter <2 mm) are predominantly concentrated at the soil surface (top 40 cm), the *Gliricidia* fine roots penetrate to greater depths (Moser *et al.*, 2010). Fine roots of both tree species extended to a maximum depth of 2.4 m.

Table 1: Soil physical and chemical properties: Bulk density, soil texture, carbon and nitrogen content, effective cation exchange capacity (ECEC) and pH (H$_2$O) of the 250 cm soil profile. The values are means ± 1 SE, n = 3.

Depth	Bulk density (g cm^{-3})	Soil Texture Sand (%)	Silt (%)	Clay (%)	Carbon (g kg^{-1})	Nitrogen (g kg^{-1})	ECEC (cmol kg^{-1})	Soil pH (H$_2$O)
Control Plots								
-5	1.27 ± 0.02	60.7 ± 1.7	25.7 ± 0.2	13.6 ± 1.6	16.6 ± 1.4	1.5 ± 0.1	7.7 ± 1.3	5.8 ± 0.3
-10	1.31 ± 0.01	54.1 ± 1.8	31.1 ± 2.4	14.8 ± 1.3	10.7 ± 1.3	1.0 ± 0.1	6.6 ± 0.6	5.6 ± 0.1
-20	1.33 ± 0.02	55.1 ± 1.0	28.3 ± 0.9	16.5 ± 0.5	6.4 ± 0.1	0.6 ± 0.0	7.3 ± 1.3	5.9 ± 0.3
-40	1.31 ± 0.02	53.9 ± 0.0	25.5 ± 1.2	20.6 ± 1.2	4.2 ± 0.3	0.4 ± 0.0	5.3 ± 0.8	5.7 ± 0.0
-75	1.36 ± 0.08	58.6 ± 2.8	22.2 ± 2.6	19.2 ± 1.8	3.4 ± 0.3	0.4 ± 0.0	7.5 ± 1.9	5.9 ± 0.0
Roof Plots								
-5	1.23 ± 0.02	59.6 ± 0.9	28.4 ± 1.8	12.1 ± 2.7	16.3 ± 2.4	1.6 ± 0.2	9.9 ± 1.2	6.0 ± 0.1
-10	1.26 ± 0.02	55.9 ± 1.1	28.2 ± 1.8	16.0 ± 1.1	14.5 ± 2.9	1.3 ± 0.2	9.0 ± 0.3	6.4 ± 0.1
-20	1.30 ± 0.0	56.2 ± 3.0	28.1 ± 2.6	15.6 ± 0.4	7.7 ± 1.1	0.7 ± 0.1	7.9 ± 0.1	6.3 ± 0.0
-40	1.32 ± 0.04	56.1 ± 1.7	27.4 ± 2.6	16.6 ± 1.6	4.6 ± 0.1	0.4 ± 0.0	5.6 ± 0.2	6.0 ± 0.1
-75	1.37 ± 0.01	57.3 ± 1.2	23.4 ± 1.5	19.3 ± 0.9	3.3 ± 0.2	0.4 ± 0.0	7.9 ± 2.5	5.8 ± 0.3

2.2 *Experimental design*

We established the experiment in a stratified random design using six plots in a one hectare area. Each plot was 40 x 35 m in dimension. Three plots were left undisturbed (control) while three treatment plots, hereafter called "roof plots", were used to simulate drought conditions. In the "roof" plots we built a transparent roof below the plantation canopy to divert throughfall away from the plot. The roof was built at a height of approximately 1.2 m and consisted of approximately 1500 individual bamboo panels

(0.5 x 4.6 m), which were covered by polyethylene plastic sheets. The roof was initially 60 % closed, with small gaps located around the tree stems and between some panels. In January 2008, the roof closure was further increased to approximately 80 %, by building smaller panels in order to close some of the bigger gaps. Runoff was diverted into a series of wooden, plastic lined gutters and channelled down-slope of the plot. Every two weeks leaf litter that accumulated on the roof panels was transferred back to the soil surface. Temperature, humidity and incident radiation under the panels were unaffected by the establishment of the roof. Along the perimeter of each plot we dug a 0.4 m trench and lined it with plastic so as to prevent lateral and surface water flows from entering the plots.

All measurements were made within a 'core zone' (30 x 25 m) in the plot, leaving a 5 m buffer zone along the inside of the plot boundary to avoid edge effects. Per plot one central soil pit (0.8 m width $\times$ 1.6 m length $\times$ 3.0 m depth) was dug and equipped with gas samplers, thermocouples and soil moisture probes. Three parallel transects per plot were set up within the 'core zone' for soil CO_2 flux measurements.

The experiment began on 27 January, 2007 with a one month (33 days) baseline evaluation phase (pre-treatment) during which conditions prior to roof closure were evaluated. The roof was closed on 1 March, 2007 and remained closed for 13 months (404 days). After the roof opening on 10 April, 2008 measurements continued for an additional five months to 27 August, 2008 (141 days) to monitor the recovery of the ecosystem.

2.3 Soil surface CO_2 efflux measurements

We determined the soil surface CO_2 efflux (soil respiration) using dynamic closed chambers (Parkinson, 1981, Norman *et al.*, 1992). At each plot, two circular polyvinyl chloride (PVC) chamber bases (0.045 m² area, 0.15 m height) were deployed in each of three parallel transects. In total six chambers were established per plot. Chamber bases were embedded 1 - 2 cm into the soil surface. At each chamber base we removed all emergent vegetation prior to measurement, and fanned the air above the chamber for at least one minute in order to bring the soil surface CO_2 concentrations to near atmospheric concentrations. We also measured the chamber height at three places around the chamber base to get a good estimate of air volume within the chamber headspace. Measurements entailed attaching a chamber hood (12 cm height) tightly to the chamber base. Air in the headspace was subsequently circulated by a small battery-operated pump at a rate of 0.8 L min^{-1} between the chamber and an infrared CO_2 gas analyzer (IRGA) (LI-800; Li-Cor Inc., Lincoln, NE, USA). The chamber was closed for 5 min 30 sec. Atmospheric

pressure was maintained within the chamber during measurements by using a small metal vent (0.1 cm in diameter and 2.5 cm length) installed on top of the chamber hood. Carbon dioxide concentrations were recorded every 5 seconds using a datalogger (Campbell CR800). A two point calibration of the infrared CO_2 gas analyzer was done in the laboratory between measurement campaigns. The first point calibration was with a 'zero' standard gas, which was created by removing CO_2 from the air by running air in a loop through a scrubber column of soda lime (4-8 mesh). The second point calibration was made using a CO_2 standard gas (700 ppm, Deuste Steininger GmbH, Mühlhausen, Germany), while a third CO_2 standard gas (356 ppm, Deuste Steininger GmbH, Mühlhausen, Germany) was used to test the quality and accuracy of the calibration.

Soil respiration flux was calculated from a 2.5 minute time window during which CO_2 concentrations increased linearly; the coefficient of determination (R^2) usually exceeded 0.993. Simultaneous to CO_2 efflux sampling we measured soil and air temperature with a handheld electronic thermometer (Greisinger GMH 3210) with a 12 cm measurement probe, and soil moisture using a portable TDR (Campbell Scientific Hydrosense – CS620) unit at 3 points around the chamber base. Measurements were made every two weeks between 8 am and 5 pm. The sequence in which plots were measured was randomized during each sampling campaign to minimize effects from diurnal fluctuations. In total, 36 soil respiration measurements were made per sampling campaign using the portable infrared CO_2 gas analyzer. During the experimental period we carried out 47 measurement campaigns. Due to an equipment failure with the IRGA we did not measure soil respiration in August 2007.

To study the contribution of leaf litter to CO_2 efflux, we randomly selected six experiment chambers in the control plots. At each of the selected sites, two additional chambers were installed directly adjacent to the 'main' chamber (<1 m away). We removed litter from one chamber and placed it into the second chamber. The 'main' chamber was left undisturbed and used as a control. The difference in CO_2 efflux between the three chambers was compared. Measurements were made during 36 measurement campaigns.

2.4   Soil air CO_2 concentrations and soil moisture depth profiles

Gas samples for CO_2 concentration analyses were collected from one central soil pit per plot. Samples were taken on a bi-weekly basis in tandem with the soil respiration measurements. The gas samplers consisted of thin stainless-steel tubes (1 mm inner

diameter), where one end was perforated with small holes and the other end was fitted with an airtight septum holder. The samplers were inserted horizontally into the soil profile at 10, 20, 40, 75, 150 and 250 cm depths. Samplers in the top 75 cm were 1 m in length, while the samplers inserted at greater depths (150 and 250 cm) were slightly longer (1.5 m) to take into consideration the diffusion losses near the soil pit wall. Each sampler was equipped with a thermocouple (Type K) at its tip so that temperature could be recorded at the time of sampling with a handheld unit (Greisinger GMH 3210). Before taking a gas sample, 5 mL of air was extracted and discarded to clear the sampler of any stagnant 'dead' air. We took the gas samples by connecting a pre-evacuated, air-tight glass vial (50 mL) to the sampler's septum holder with a syringe needle and short flexible plastic tube and then opened a two-way stop valve on the glass vial to suck in the gas sample. A sample was also taken at the soil surface by sticking a polypropylene syringe (with 5 cm needle) into the ground and drawing a sample.

Samples were analyzed in a laboratory at Tadulako University in Palu, Sulawesi, within 72 hours after collection in the field. We measured the CO_2 concentration of each sample using a gas chromatograph (GC) (GC-11, Delsi Instruments, Suresnes, France) with thermal conductivity detector (TCD). Sample CO_2 concentrations were calculated by comparing the integrated peak areas to that of two known standard gas concentrations (0.07 % and 3.5 %, Deuste Steininger GmbH, Mühlhausen, Germany), to make a two point calibration.

Additional to the CO_2 concentration and temperature measurements, we also measured volumetric soil water content using time domain reflectometry (TDR) sensors (Campbell CS616) in three soil pits per plot. TDR sensors were installed adjacent to each gas sampler, in the central pit, by inserting them into the undisturbed soil at the end of a 30 cm hole dug horizontally into the soil pit wall. Soil moisture was recorded hourly using a datalogger (Campbell CR1000). Due to high rock content in the soil we could not install TDR sensors in three plots at 250 cm depth. Using undisturbed soil samples we calibrated the water content measurements using the methodology described by Veldkamp & O'Brien (2000). Volumetric water content was recalculated to soil matric potential using soil water retention curves developed by (van Straaten, unpublished data).

Soil CO_2 concentration measurements were made during 46 field campaigns, in tandem with the IRGA soil respiration measurements. One additional field campaign was missed due to a large landslide that limited access to the site with the gas sampling equipment.

2.5 CO_2 leaching losses

To determine whether the downward flux from leaching accounted for an important CO_2 exit pathway losses we calculated the amount of CO_2 dissolved in water and linked it with modeled drainage estimates. According to Henry's Law, CO_2 dissolved in water is proportional to the partial pressure of CO_2 above the solution and the CO_2 Bunsen absorption coefficient. When carbon dioxide dissolves into water it can produce two possible reactions (Eq. 1 and 2). The solubilisation of CO_2 gas:

$$CO_2 \text{ (gas)} \rightarrow CO_2 \text{ (aq)} \tag{1}$$

and hydration of CO_2 (aq) to form carbonic acid

$$CO_2 \text{ (aq)} + H_2O \rightarrow H_2CO_3 \text{ (aq)} \tag{2}$$
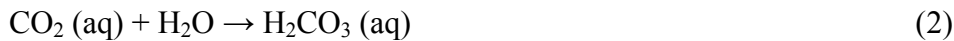
However, given the low proportion of H_2CO_3 (aq) relative to CO_2 (aq) it is possible to lump their concentrations together with Henry's law. The dissolved CO_2 was calculated as follows:

$$M - CO_2 w = CO_2 a \times VWC \times B \tag{3}$$

whereby M–$CO_2\ w$ is the CO_2 content dissolved in the liquid phase (g CO_2 m^{-3}), $CO_2\ a$ is the partial pressure of CO_2 (concentration) in the soil air (g CO_2 m^{-3}) at atmospheric air pressure, VWC is the soil's volumetric water content and B is the Bunsen solubility coefficient for CO_2. The Bunsen coefficient is the volume of gas that can be absorbed by one cubic meter of water at standard atmospheric air pressure, at 24°C, the CO_2 Bunsen coefficient is 0.7771 g m^{-3}.

Dissolved CO_2 was calculated for the gas samples taken at 250 cm soil depth and interpolated to give daily values of dissolved CO_2 throughout the duration of the experiment period. Subsequently, dissolved CO_2 was multiplied with daily modeled soil water drainage to determine CO_2 leaching losses. Soil drainage from roof and control plots were modeled using HYDRUS 1D (Šimůnek *et al.*, 2008) with measured transpiration rates, net precipitation and soil water contents as input. The method has been described in greater detail in Köhler *et al.*(in preparation). Leaching losses were calculated only from

10 February, 2007 to 5 June, 2008 because of the shorter time frame in which soil water drainage was modeled.

2.6   Isotope analysis

To identify the origin of the high CO_2 concentrations in deep soil, $^{13}CO_2$ isotope signatures were measured. One soil air sample was taken from each plot at 250 cm depth, stored in airtight, stainless steel vials and transported to the Centre for Stable Isotope Research and Analysis (KOSI, Georg-August-University of Goettingen, Germany) for analysis using a Isotope Ratio Mass Spectrometer (Finnigan MAT Delta Plus, Bremen, Germany). The isotopic signature can indicate whether the CO_2 was produced either biologically or from geological origins.

2.7   Data analysis

We divided the experiment into three time periods: pre-treatment, treatment and post-treatment. Throughout the experiment, roof plot measurements were compared to adjacent control plots to decipher roof plot ecosystem drought response from normal fluctuations. Individual soil CO_2 efflux chamber measurements were averaged for each plot at each measurement date and logarithmically transformed to normalize data distributions. The significance of the drought effect difference was tested using mixed linear effects models for the three time periods mentioned above, the overall experiment period (from start to finish) and an extra time interval during the last three months of the treatment period during which drought effects were most pronounced. In the model, the desiccation treatment was considered a fixed effect while the measurement day (from day 1 to day 579) and plot were considered as random effects. Differences were considered significant if $P \leq 0.05$. Additionally, temporal autocorrelation in this time series CO_2 flux dataset was corrected for by using a first order autoregressive model.

The relationship between soil CO_2 efflux and soil moisture (at 10 cm), soil surface temperature, *Gliricidia* and cacao sap flux densities, and chamber distance from tree stem were tested with linear regressions. All statistical analyses were done using the statistical package R version 2.8.1 (R Development Core Team, 2008).

3   Results

3.1   Volumetric soil water content and soil temperature

During the pre-treatment phase, volumetric soil water content of all six experiment plots were in the same range for each respective sampling depth (Fig. 1c). Approximately ten days after roof closure, soil water contents began to diverge between the control and roof plots. Soil moisture contents in the plots under the roof decreased simultaneously at all depths, apart from the depth of 250 cm depth which began drying out only after a period of two and a half months. Although gaps in the roof did allow some throughfall to enter, the water recharge was limited to the upper soil layers and was never enough to recharge the soil under roof to control plot levels. A natural drought in January – February 2008 reduced soil water contents in both roof and control plots. The drying effect was recorded down to 250 cm depth in the control plots. Minimum soil water contents in the roof plots were experienced during this dry spell. Upon roof opening in April 2008, soil water contents in the roof plots quickly rose to near control plot levels.

Soil surface temperature exhibited little fluctuation throughout the duration of the experimental period, ranging from a minimum temperature of 21.8°C to a maximum temperature of 24.8°C. The average soil temperature at 5 cm depth was unaffected by the roof installation, measuring 23.2 ± 0.8°C and 23.0 ± 0.7°C (mean $\pm$ SD) for the roof and control plots respectively. At 250 cm depth, soil temperatures were slightly higher than at the surface and averaged 24.0 ± 0.4°C (mean $\pm$ SD).

3.2   Soil surface CO_2 efflux

Soil surface CO_2 efflux was highly variable in both space and time. Spatially, the average coefficient of variation of the 18 roof plot and 18 control plot chambers was 52 % and 46 % respectively over the period of the experiment. The temporal coefficient of variation for individual chamber measurements was slightly lower in the control plots (40 %) in comparison to the treatment plots (53 %).
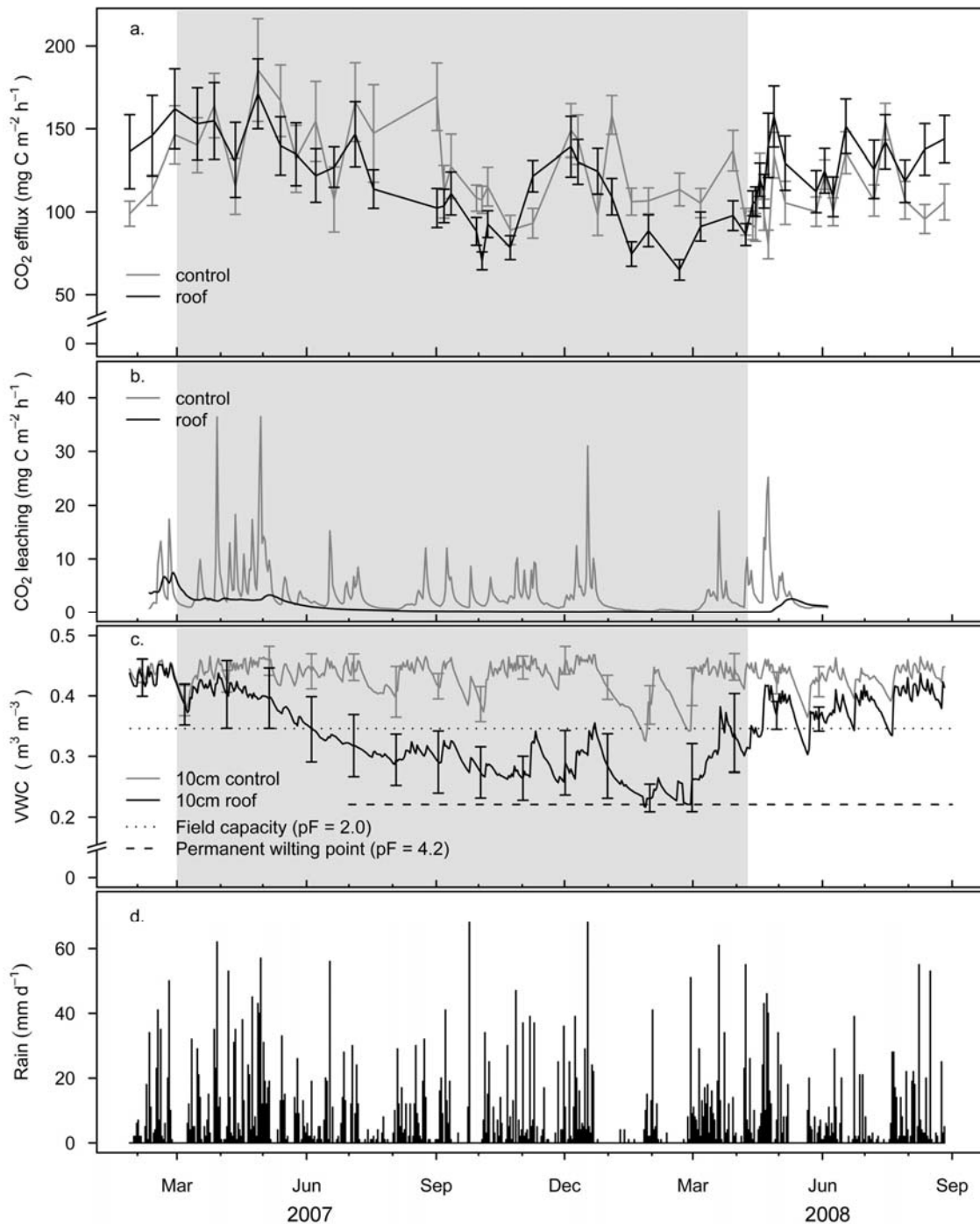
Figure 1: Soil CO_2 efflux, soil CO_2 leaching, volumetric water content and daily precipitation. (a) Average soil surface CO_2 efflux in control and roof plots, (b) average soil CO_2 leaching losses in control and roof plots, (c) average volumetric water content at 10cm soil depth in control and roof plots and (d) daily precipitation. Error bars indicate ±1 SE. The shaded area indicates the period of roof closure.

During the pre-treatment phase, soil CO_2 efflux measurements were slightly higher in the roof plots as compared to the control, though not statistically significant (P = 0.13) (Fig. 1a and Table 2). Following roof closure in March 2007, soil respiration rates in the roof plots began a slow decline that lasted until late October 2007. From early November

until mid December 2007, roof plot respiration rates experienced a short lived peak followed by a second decline during a two month natural drought. Respiration rates reached a minimum level in late February 2008 and thereafter remained low until roof opening in April 2008. During the treatment period the control plots did not exhibit any distinct temporal trend although soil CO_2 efflux variability was highest during the first half year and less so thereafter.

The overall differences in average soil CO_2 efflux between the control and the roof plots were relatively minor. Soil CO_2 efflux declined only slightly in the control plots in comparison to the roof plots. On average, roof plots respired 13 % less than the control plots, although this difference was not statistically significant ($P = 0.16$). In the last three months of the simulated drought the onset of a natural dry spell in combination with improved roof closure resulted in a further decline in the soil CO_2 efflux. During this time the roof plots averaged 75 % of the control soil respiration, a decline of 25 % ($P < 0.05$). Immediately upon roof opening, in April 2008, we measured a flush of soil CO_2. Within three days, soil CO_2 efflux exceeded the control plots by more than 15 %. Over the next five months the average roof plot CO_2 efflux remained consistently above control plot efflux levels, although the treatment means were not significantly different. One roof plot chamber was removed from the analysis shortly after roof opening as it suddenly began producing very high CO_2 fluxes.

The cumulative CO_2 respired from control and roof plots was not significantly different, indicating the drought had a CO_2 neutral effect. The cumulative CO_2 flux from the 579-day experiment was 17.5 ± 0.75 Mg C ha^{-1} and 16.6 ± 0.74 Mg C ha^{-1} for the control and roof plots respectively. Annually this equates to 11.1 ± 0.5 Mg C ha^{-1} yr^{-1} for the control plot and 10.5 ± 0.5 Mg C ha^{-1} yr^{-1} for the roof plot.

Although the overall drought response in the roof plots was relatively moderate, 11 of the 18 efflux chambers in the roof plots exhibited stronger drought effects than the others (Fig. 3). Drought effects were most pronounced at chamber sites already producing high CO_2 before the roof closure. We used the coefficient of determination (R^2) of a linear regression between CO_2 efflux and the soil moisture as an index of drought response (hereafter called the "drought response index") and plotted it spatially (Fig. 2). The drought response appeared to be localized, as some chamber sites measured strong relationships to soil water content changes (up to $R^2 = 0.70$), while other chambers often located nearby measured little to no response to decreasing soil water contents.

Over the course of the 19-month measurement period, no distinguishable seasonal patterns in either precipitation (Fig. 1d) or in air temperature were measured (data not shown).
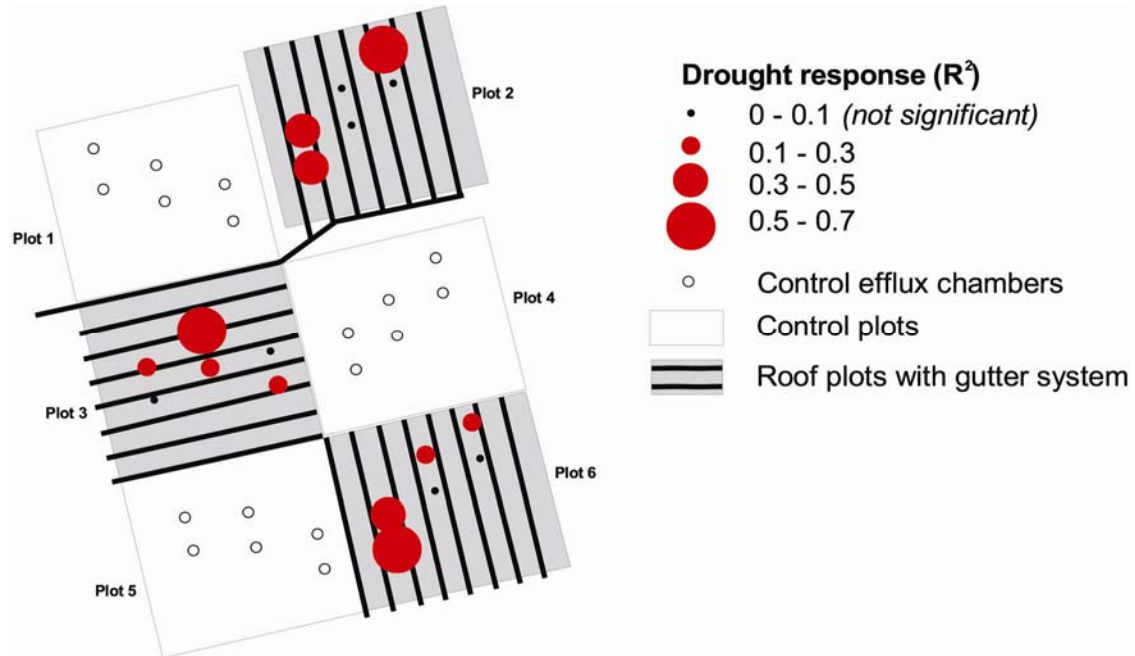
Figure 2: Drought responsiveness map. Schematic of cacao agroforestry plot layout and response of CO_2 flux chambers to soil water content changes. The coefficient of determination (R^2) for the CO_2 efflux to volumetric water content was used as index of how strong a chamber reacted to changes in soil moisture.
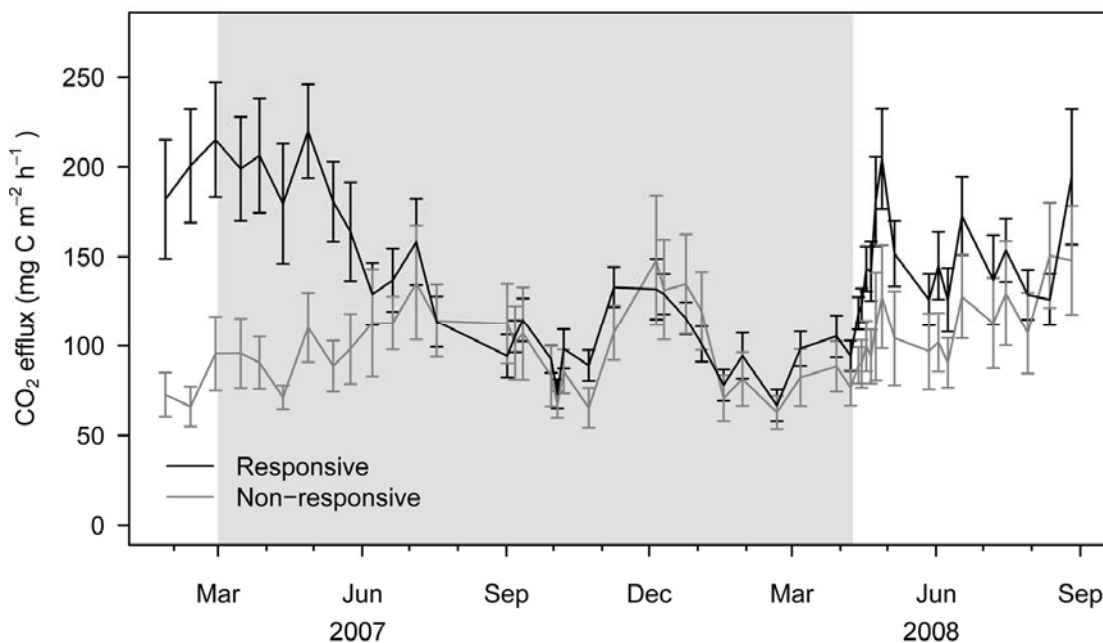
Figure 3: Drought responsive versus non-responsive CO_2 efflux comparison in the roof plots. Error bars indicate ± 1 SE. The shaded area indicates the period of roof closure.

Table 2: Experiment soil surface CO_2 efflux (mg C m^{-2} h^{-1}) and soil air CO_2 concentrations (%) for different soil depths for the pre-treatment, treatment, post-treatment. Mean value ± 1 SE. n = number of sampling campaigns.

		Pre-treatment			Treatment			Post-treatment			Entire experiment period	
	n	Control	Roof	n	Control	Roof	n	Control	Roof	n	Control	Roof
CO_2 efflux (mg C m^{-2} h^{-1})	3	118.0 ± 15.6	142.5 ± 31.8	28	131.8 ± 7.6	114.7 ± 6.8	16	112.0 ± 6.4	129.4 ± 8.5	47	126.2 ± 5.4	119.5 ± 5.4
Soil CO_2 concentrations (%)	3			28			15			46		
-5 cm		0.4 ± 0.2	0.5 ± 0.3		1.3 ± 0.2	0.6 ± 0.0		1.3 ± 0.2	1.2 ± 0.1		1.2 ± 0.1	0.8 ± 0.1
-10 cm		3.7 ± 0.9	5.1 ± 0.6		2.4 ± 0.2	1.2 ± 0.1		2.8 ± 0.2	2.7 ± 0.1		2.6 ± 0.2	1.8 ± 0.1
-20 cm		5.7 ± 0.4	6.0 ± 0.5		4.0 ± 0.2	1.7 ± 0.2		5.0 ± 0.2	3.8 ± 0.1		4.4 ± 0.1	2.4 ± 0.1
-40 cm		6.1 ± 0.5	7.8 ± 0.4		4.9 ± 0.2	2.4 ± 0.2		5.5 ± 0.3	4.5 ± 0.1		5.1 ± 0.2	3.2 ± 0.2
-75 cm		7.1 ± 0.5	8.5 ± 0.4		6.3 ± 0.2	3.2 ± 0.2		7.4 ± 0.3	5.5 ± 0.1		6.6 ± 0.2	4.0 ± 0.2
-150 cm		9.9 ± 0.3	10.3 ± 0.4		9.2 ± 0.2	5.7 ± 0.3		10.1 ± 0.2	7.6 ± 0.2		9.5 ± 0.1	6.3 ± 0.2
-250 cm		12.4 ± 0.2	12.3 ± 0.7		11.6 ± 0.2	8.7 ± 0.3		12.2 ± 0.1	10.6 ± 0.1		11.8 ± 0.1	9.3 ± 0.2

3.3   Controls regulating CO_2 efflux

Soil CO_2 efflux exhibited a strong relationship with soil moisture. CO_2 efflux peaked under intermediate soil moisture contents (between pF 1 and 2) and decreased when conditions became either wetter ($R^2 = 0.34$, $P < 0.01$), or drier ($R^2 = 0.71$, $P < 0.01$) (Fig. 4). The rate of change (slope) at the wet end of the moisture spectrum was steeper than at the drier end. Soil temperature had little effect on soil CO_2 efflux. Only in the control plots did we find a significant, but weak, positive relationship with soil temperature ($R^2 = 0.16$, $P < 0.01$). There was no relationship found between soil moisture and soil temperature.
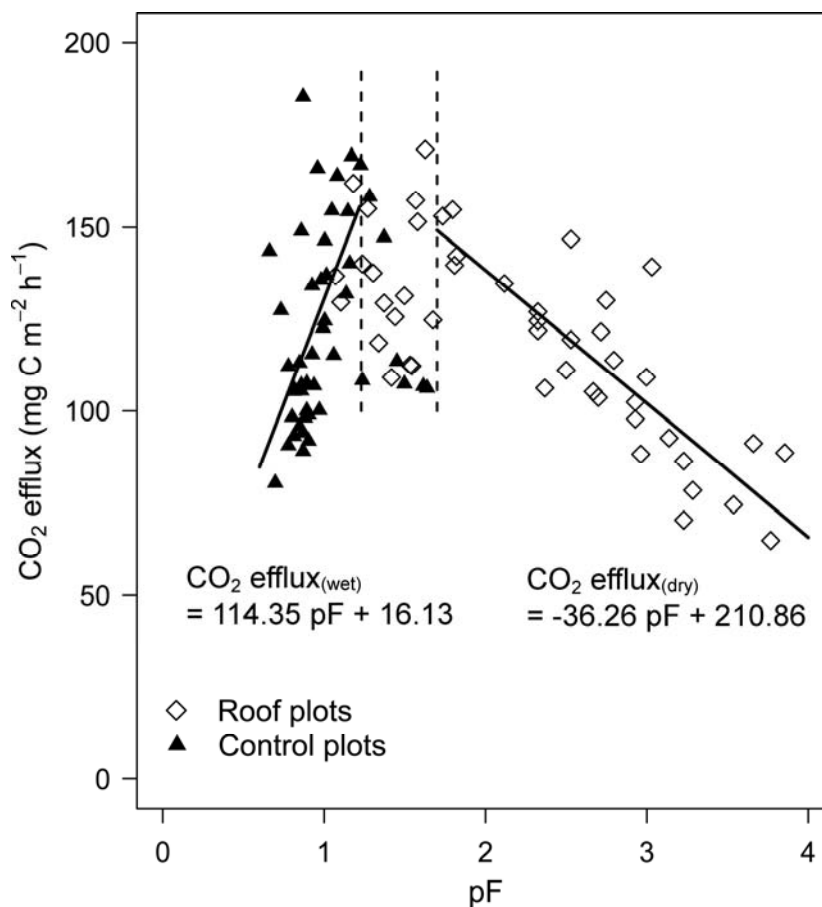
Figure 4: Relationship between soil water potential (pF) and soil CO_2 efflux (Wet relationship: $R^2 = 0.34$, $P < 0.001$, Dry relationship: $R^2 = 0.71$, $P < 0.001$) showing the average soil CO_2 efflux measurements from roof and control plots for each measurement campaign. Each point represents the average of 18 CO_2 efflux measurements. Soil moisture was measured using TDR sensors from three soil pits per plot embedded horizontally at 10 cm soil depth.

A weak diurnal pattern was detected in soil respiration, whereby CO_2 efflux was lowest early in the early morning before 8 am and rose steadily throughout the day reaching a

maximum in the late afternoon between 4 and 6 pm (Table 3). No night-time measurements were made.

Table 3: Diurnal soil CO_2 efflux, soil temperature and air temperature during daytime hours. The mean values are ± 1 SE.

	Time	n	Roof Plot Soil CO_2 flux [mg C m^{-2} h^{-1}]	n	Control Plot Soil CO_2 flux [mg C m^{-2} h^{-1}]	Soil temperature [°C]	Air temperature [°C]
Early morning	06:00-08:00	19	95.0 ± 12.5	9	107.6 ± 12.6	23.1 ± 0.2	22.7 ± 0.5
Mid morning	08:00-10:00	238	110.0 ± 3.8	267	109.3 ± 3.3	22.9 ± 0.0	24.3 ± 0.1
Late morning	10:00-12:00	318	124.0 ± 4.0	292	118.6 ± 3.6	23.0 ± 0.0	26.6 ± 0.1
Early afternoon	12:00-14:00	149	127.9 ± 6.0	141	125.3 ± 6.0	23.3 ± 0.0	27.6 ± 0.1
Mid afternoon	14:00-16:00	71	132.8 ± 9.6	85	142.0 ± 8.6	23.8 ± 0.1	26.6 ± 0.2
Late afternoon	16:00-18:00	36	131.9 ± 12.8	36	138.3 ± 12.8	24.2 ± 0.1	25.4 ± 0.1

Soil respiration was found to decrease with distance from cacao tree stems ($R^2 = 0.22$, $P < 0.01$), but showed not relationship with distance from *Gliricidia* trees. CO_2 efflux measurement chambers were established between 1.1 and 2.1 meters from the nearest tree. In the roof plots, the CO_2 drought response index declined with distance from cacao tree stems ($R^2 = 0.23$, $P = 0.053$), but showed no relationship with distance to *Gliricidia* tree stems.

3.4   *Leaf litter respiration*

The leaf litter layer contributed on average 16.8 % of the total respired CO_2 efflux. Although we did not measure the moisture of the litter layer directly there is a strong indication that respiration rates were positively related to the moisture regime of the leaf litter. Soil moisture probes located at 10 cm soil depth showed a positive linear relationship ($R^2 = 0.20$, $P < 0.01$) between soil moisture and the leaf litter CO_2 efflux contribution. In other words, when conditions were dry CO_2 efflux from the litter was low and did not contribute much to the overall soil flux (~3 - 4 % of the total flux). However, when conditions were wet, leaf litter CO_2 efflux increased and became an important CO_2 production source contributing up to 40 % of the overall CO_2 efflux. The leaf litter CO_2 contribution to the overall control plot CO_2 flux over the duration of experiment is shown in Figure 5.
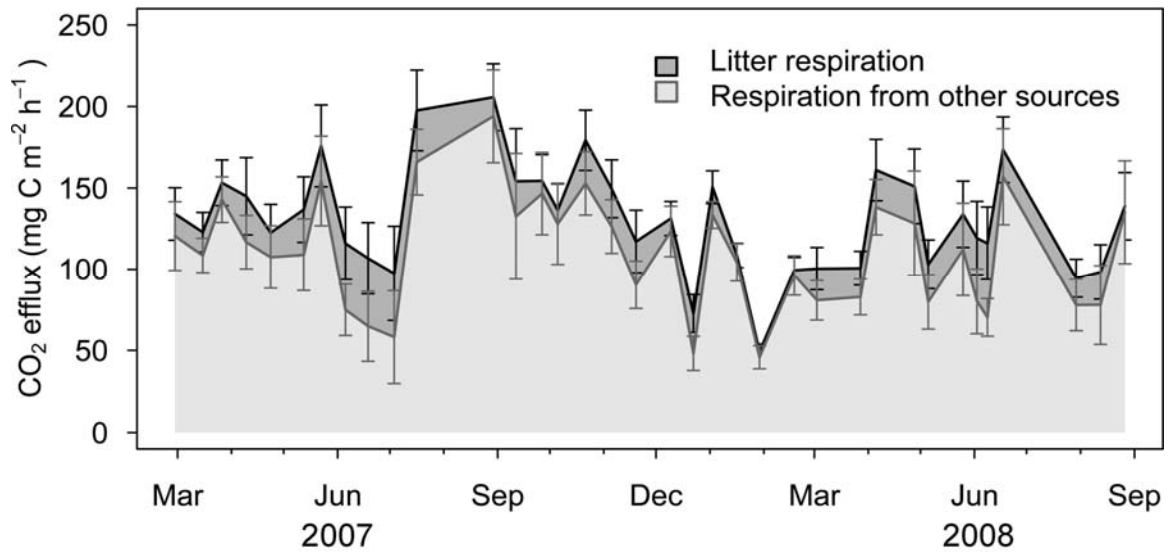
Figure 5: CO$_2$ efflux from leaf litter contribution study in the control plots. The dark grey colour indicates the CO$_2$ production derived from leaf litter, while the light grey colour denotes the CO$_2$ production from within the soil profile from other sources. The error bars indicate the standard error of the six measurements per sampling date.

3.5 Soil profile CO$_2$ concentrations

Soil CO$_2$ concentrations increased with soil depth, displaying an exponential shape in concentration rise (Table 2), where concentrations near the soil surface (0 - 10 cm) were relatively low and increased rapidly with depth (between 20 - 75cm depth) and finally approached an asymptote at deeper soil depths (150 - 250 cm). Average CO$_2$ concentrations in the control plots over duration of the experiment period at 250 cm were 11.8 % - this is more than 300 times higher than atmospheric CO$_2$. The highest recorded CO$_2$ concentration was 15.3 % in October 2007 in one of the control plots.

During the pre-treatment period soil CO$_2$ concentrations in the control and treatment plots were similar for each respective soil depth (Fig. 6). Upon roof closure, CO$_2$ concentrations in the roof plots began to decline in tandem with the drying out of the soil profile. CO$_2$ concentrations declined steadily over the 13-month treatment period and reached a minimum level in the last month of the induced drought. CO$_2$ concentrations reached lows of between 17 % (at 10 cm depth) and 52 % (at 250 cm depth) of the control plot levels. During the driest period of the simulated drought the soil CO$_2$ concentration depth profile was nearly linear in shape, supposedly saturating at a deeper depth than from which we sampled. Although CO$_2$ concentrations in the control plots remained relatively constant throughout the treatment period, a sharp drop was measured at all soil depths in January – February 2008, during a phase of natural drought. When we opened the roof in

April 2008, CO_2 concentrations rose quickly; within a one month period CO_2 concentrations at all depths rose to near control plot levels whereby CO_2 concentrations at shallower depths rebounded faster than in the subsoil. Thereafter, CO_2 concentrations levelled off, and remained lower than the control plot until the end of the experiment in August 2008.

The δC^{13} isotope signature of the six CO_2 gas samples was -23.63 ± 0.19 ‰ (mean $\pm$ SD) indicating that the CO_2 present in the soil profile is biologically produced and most likely produced by C_3 plants – e.g. cacao and *Gliricidia*.
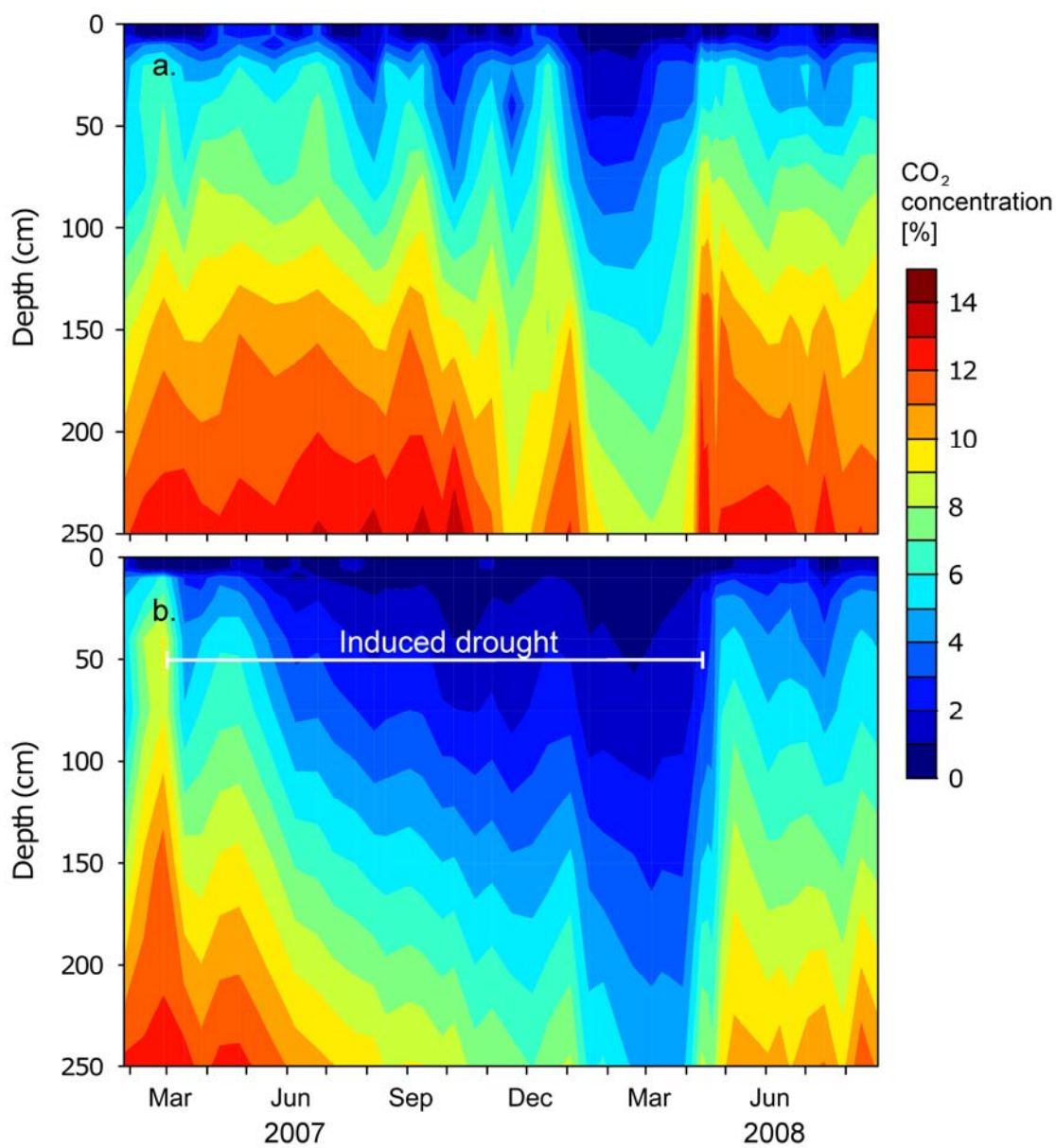

Figure 6: Isopleths of average soil CO_2 concentrations (%) in the soil profile of (a) control plots and (b) roof plots in soil air throughout the experiment period.

3.6 CO_2 leaching losses

The control plots on average stored 93 % of the total carbon dioxide in soil water as aqueous CO_2, while the remaining 7 % was present in the gaseous phase. In the roof plots, on average 65 % of the total CO_2 was dissolved in soil water.

Dissolved CO_2 drainage losses during the experiment period are shown in Fig. 1b. In the control plots CO_2 leaching losses spiked during periods of high drainage. They reached as high as 36.5 mg C m^{-2} h^{-1} (15 % of the total CO_2 flux), on a single day. However, on average the CO_2 drainage in the control plots remained low at 3.5 mg C m^{-2} h^{-1}, which is 2.6 % of the overall surface flux. In the roof plots, CO_2 leaching was even lower given the drier soil profile and reduced drainage discharge. During the treatment period soil water drainage approached zero. In these plots the CO_2 leaching losses were on average 0.82 mg C m^{-2} h^{-1}.

4   Discussions

4.1 CO_2 fluxes in a cacao agroforestry system

As far as we are aware this study represents the first in situ measurements of soil CO_2 dynamics of a cacao agroforestry ecosystem. Measured CO_2 efflux rates indicate that the ecosystem is very productive as respiration rates were within or slightly below the range measured in tropical forest ecosystems in Asia (Adachi *et al.*, 2006, Ohashi *et al.*, 2008), and in Latin America (Davidson *et al.*, 2008, Davidson *et al.*, 2000, Schwendenmann *et al.*, 2003, Sotta *et al.*, 2006).

Prior to roof closure, three pre-treatment one-day field campaigns showed no difference in the average soil respiration rates between the control and roof plots. Roof plot respiration averages were slightly higher than the control and are attributed to the higher bulk densities in the control plots.

The main controlling variable driving soil CO_2 efflux in this ecosystem was soil moisture. Soil respiration peaked at intermediate soil water contents and declined under both wetter and drier conditions (Fig. 4). Unlike the gradual decline observed in soil respiration when conditions got drier (as was observed in the roof plots and will be discussed later), soil respiration rates in the control plots often plummeted when moist soil became slightly wetter. This is evident by the steep slope shown at wet end of the moisture spectrum. As a result, the CO_2 flux in the control plots exhibited strong efflux fluctuations

with minor changes in soil moisture. The reduction in soil CO_2 efflux under the saturated conditions may be a result of a diffusion block that prevented CO_2 from exiting the soil through the saturated pore space, and / or prevented oxygen from diffusing into the soil – subsequently creating anaerobic conditions (Luo and Zhou, 2006).

CO_2 production from the leaf litter was sensitive to moisture conditions. When external conditions were wet, the litter layer could contributed as much as 40 % of the total CO_2 efflux, however when conditions were dry, the CO_2 contributions from the litter layer was nearly zero percent.

Soil temperature displayed a slightly positive relationship with soil CO_2 efflux (data not shown). The temperature influence was however not very predominant given the small temperature variation (in total 3°C) experienced during the 19 month experimental period. In contrast to studies conducted in rainforests in the Amazon basin (Wofsy *et al.*, 1988) and in Costa Rica (Schwendenmann *et al.*, 2003) the influence of solar radiation on plant photosynthesis was not measured in our soil respiration measurements for this site.

Dissolved CO_2 leaching beyond 250 cm soil depth proved to be only a minor CO_2 exit flux (Fig. 1b). Considering the high proportion of CO_2 stored in the liquid phase, the overall CO_2 leaching flux from below 250 cm was relatively low (3.5 and 0.8 mg C m^{-2} h^{-1} for control and roof plots respectively). This is in line or slightly higher than CO_2 leaching fluxes reported by Schwendenmann and Veldkamp (2006) and Johnson *et al.* (2008). The diffusion of carbon dioxide through soil water along the CO_2 concentration gradient is considered negligible since liquid phase diffusion (in free water) is more than 8,000 times slower than CO_2 transport through free air (Moldrup *et al.*, 2000).

4.2   *Drought effects on soil CO_2 efflux*

In contrast to our initial hypotheses, the cacao agroforestry system did not exhibit a strong CO_2 efflux response to the induced drought. Instead, the average CO_2 efflux declined moderately (13 %) in the roof plots in comparison to the adjacent control plots during the simulated drought. The overall muted CO_2 efflux response may be attributed to a number of reasons:

The nature in which CO_2 efflux responds to soil moisture may have obscured effect differences between control and roof plots. As has been observed in earlier studies (Davidson *et al.*, 2000, Schwendenmann *et al.*, 2003, Sotta *et al.*, 2006), a pronounced peak of soil CO_2 emission was measured at intermediate soil water contents and declined

under both drier and wetter conditions (Fig. 4). Therefore, when we compare average soil respiration rates between roof plots and control plots during a time when the roof plots were dry and when the control plots were saturated, not only would the measured respiration rates in the roof plots be depressed because of the induced drought, but respiration rates in control plots would also be lower because of the high soil water content.

We have several indirect indications that different CO_2 sources reacted differently to drought stress. The first indirect indication comes from the spatial variability of soil respiration across the project area. While eleven efflux chamber sites in the roof plots showed relatively strong declines in soil CO_2 efflux as the soil dried out, the other seven efflux chambers, often just a few meters away, exhibited little to no reaction (Fig. 2 and Fig. 3). This localized drought response is indicative of the contrasting processes taking place directly below the respective chambers. The second indirect indication was that soil CO_2 efflux from chambers that exhibited strong drought response correlated closely to the sap flux ratios of both cacao (R = 0.61, P < 0.01) and *Gliricidia* trees (R = 0.65, P = 0.01) as reported by Schwendenmann *et al.* (2010). In contrast, those chambers that did not exhibit a drought sensitive CO_2 efflux did not correlate significantly with sap flux density. Although this does not necessarily establish a causal relationship between soil CO_2 efflux and tree sap flux, it does however show that when tree metabolisms slowed down, we correspondingly measured lower CO_2 effluxes from the drought responsive efflux chambers. Our interpretation is that these drought responsive chambers, which had higher than average respiration rates even during the pre-treatment measurements, were situated above active roots and the onset of drought conditions induced tree drought stress which resulted in root respiration decreases. This is substantiated by the strong correlation between the average soil respiration prior to roof closure (pre-treatment) and the drought response index (R^2 = 0.76, P < 0.01, n = 18). This means that the high flux chambers were situated above already active CO_2 production sources, very likely active roots, which were susceptible to drought stress.

Furthermore, the drought effect on autotrophic respiration was again detected when examining the relationship between soil CO_2 efflux and the distance to tree stems. We found that the drought response index declined with distance from cacao tree stems suggesting that cacao rooting activity near the stem declined during the induced drought while further away the effect was not as pronounced. We also found that average soil CO_2 respiration rates declined with distance from cacao tree stems in both control and roof

plots. Soil compaction was excluded as a potential explanatory variable for these decreases, as bulk density cores taken at 0.25 m distance intervals outward from the tree stem to a maximum distance of 1.75 m, failed to show any systematic increases with distance (n = 6 cacao trees). Stem flow and the potentially wetter conditions around the tree base was also excluded as an explanatory variable as we did not find an evident relationship between the average soil moisture and the respective distance to the tree.

Unlike the cacao trees, we did not observe similar tree distance relationships with *Gliricidia* trees. This is thought to be primarily due to the deeper and more diffuse root architecture and rooting behaviour exhibited by *Gliricidia* fine roots (Moser *et al.*, 2010), which may have masked measurable effects with distance. A Deuterium (δD) study by Schwendenmann *et al.* (2010) found that tree water uptake was partitioned vertically in the soil horizon, where cacao accessed water from the upper horizons while *Gliricidia* explored for water in deeper soil layers.

Additionally, a root excavation exercise done by Moser *et al.* (2010) at the site, found that coarse roots of both cacao and *Gliricidia* were primarily concentrated around the tree stems while fine root (diameter < 2mm) distributions extended well into the agroforestry plantation. Other studies by Harteveld *et al.* (2008) and Kummerow *et al.* (1982) confirm that cacao fine roots extend well beyond the stem and are primarily concentrated in the uppermost 30 cm. Although overall autotrophic respiration rates appeared to decline, Moser *et al.* (2010) reported that cacao and *Gliricidia* fine root biomass remained unchanged at all soil depths to 250 cm, over the duration of the 13-month induced drought. These findings suggest that regardless of the drought stress, the trees still continued to maintain and build new fine roots required to search for available water resources.

The litter layer, as was previously mentioned, is sensitive to changes in moisture regimes. Therefore, given that the litter layer would have dried out relatively quickly, the effect on soil respiration would have also been correspondingly fast. By the end of the roof experiment, in April 2008, considerable amounts of leaf litter had accumulated on the ground of the roof plots, although leaf litter fall was unaffected by the induced drought (Schwendenmann *et al.*, 2010). This is an additional indication that decomposition rates decreased under the drier conditions.

Although we have little data to substantiate how heterotrophic CO_2 respiration from soil microorganisms in the bulk soil reacted to the drought, the results from the leaf litter study clearly show that heterotrophic respiration was sensitive to droughts.

4.3 Belowground CO_2 dynamics

Baseline carbon dioxide concentrations in deep soil air were among the highest ever reported for soils. The average CO_2 concentration at 250 cm soil depth in the control plots was 11.8 %, and peaked at 15.3 %, during the 19-month experiment. As far as we are aware of no other study has found CO_2 concentrations of this magnitude so close to the soil surface. The δC^{13} isotope signature (-23.63 ‰) confirmed that the CO_2 was produced by biological sources and most likely originated from plants having a C_3 photosynthetic pathway - such as cacao or *Gliricidia*.

The high CO_2 concentrations in soils of the cacao agroforestry ecosystem are thought to be caused by a diffusion block that prevented CO_2 molecules from travelling upward along the concentration gradient to the atmosphere. Gaseous CO_2 diffusion was slowed down by the soil medium's high bulk density (low porosity), high concentration of coarse rock fragments as well as soil water. Each of these components would have increased the tortuousness of the gas pathway to the soil surface. During wet conditions CO_2 concentrations were high in the soil air, as the pore-space would have been saturated with water and resulted in slow diffusion. However, as soon as the soil dried out the CO_2 concentrations began to decline, as there were more open air filled pore-spaces available for CO_2 diffusion. This trend is apparent in both the roof plots (where we artificially manipulated the soil moisture) and in the control plots during a natural drought in January – February 2008 (Fig. 6). In and of itself, the soil air CO_2 concentrations do not say very much about the soil carbon allocation dynamics, but highlight the CO_2 storage capacity of the soil.

Attempts to determine CO_2 production shifts with time vertically within the soil profile by modelling CO_2 production from soil air CO_2 concentrations with a one dimensional gas transport model were not successful. We believe that due to the high rock fragment content and the heterogeneous composition of the sub-soil various assumptions required by the gas transport model were not met.

4.4 Rewetting phases

In November 2007, approximately halfway through the simulated drought period, soil respiration rates in the roof plots (at both drought responsive and non-responsive chamber sites) experienced a short lived rebound that lasted for approximately two months. The rebound coincided with two small rewetting peaks measured in the uppermost 40 cm of the

soil, during an extended period of intense rain showers. During this time it is speculated that the CO_2 flush resulted from a sudden burst in root activity and a pulse of microbial activity which mineralized built up organic compounds.

The second and planned rewetting phase took place after the first rain showers following the roof opening in April 2008, at which time we measured a flush of CO_2 from the soil surface that lasted for approximately two weeks. During this time the labile carbon stocks that had accumulated during the induced drought (including dead roots, accumulated litter and other organic compounds) probably mineralized. Additionally, tree roots may have responded to the favourable soil moisture conditions and at minimum resumed normal activity, or extended their root network. Schwendenmann *et al.* (2010) reported that sap flux densities of both cacao and *Gliricidia* trees recovered quickly.

Beyond the initial two week flush, average soil CO_2 fluxes remained slightly but not significantly above control plot averages until the end of the measurement period in late August 2008. This is likely due to two reasons: 1) the time the ecosystem required to return to equilibrium – for trees to extend their root systems and for microorganisms to decompose built up carbon stocks, or 2) it may reflect the effect of slightly higher bulk densities in the control plots.

5   Conclusions

Although, there were evidently some carbon reallocation responses to drought periods in the cacao agroforestry ecosystem, the net effect on soil CO_2 production and emission over the duration of the experiment was neutral. During the 13-month treatment phase, we observed slight decreases in soil respiration in the roof plots likely due to localized changes in root activity, and declines in decomposition rates both above and belowground. The decline in soil respiration in the treatment period were however compensated for during the post-treatment phase (after roof opening), when accumulated labile carbon stocks, both above and below ground mineralized, and when trees recovered from their drought stress.

CHAPTER 3

EFFECTS OF A SIMULATED DROUGHT ON SOIL CO_2 PRODUCTION IN A SUB-MONTANE TROPICAL FOREST IN CENTRAL SULAWESI, INDONESIA

A REVISED VERSION HAS BEEN SUBMITTED TO GLOBAL CHANGE BIOLOGY

EFFECTS OF A SIMULATED DROUGHT ON SOIL CO_2 PRODUCTION IN A SUB-MONTANE TROPICAL FOREST IN CENTRAL SULAWESI, INDONESIA

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Abstract

Drought response on soil CO_2 production dynamics was examined in a sub-montane tropical rainforest (1050 m.a.s.l.) in central Sulawesi, Indonesia. A large-scale throughfall displacement roof was built in the ecosystem understory to simulate drought conditions. During the 31 month experiment, soil CO_2 production was measured biweekly both vertically within the soil profile to 2.5 m depth by using a one dimensional gas diffusion model and also spatially across the plot area by measuring surface CO_2 efflux at permanently embedded chambers distributed throughout the project area. We additionally partitioned CO_2 production into leaf litter, belowground heterotrophic (microbial) and autotrophic (root) respiration sources. During the 24.5 month induced drought the sub-montane tropical rainforest experienced a severe decrease in soil CO_2 production. Soil CO_2 efflux decreased by an average of 39 % in comparison to the control during induced drought period. Soil moisture, the main variable controlling CO_2, exhibited a strong positive linear relationship with soil CO_2 production (R^2 = 0.72). A two phase ecosystem drought response was observed. During the first phase, which lasted nine months, leaf litter respiration declined as did the CO_2 production between 30 and 70 cm soil depth. During the second phase of the experiment (the next 16 months) drought conditions intensified further and belowground CO_2 production from heterotrophic and autotrophic sources decreased at all soil depths. Leaf litter respiration remained negligible. Recuperation after the drought was slow and did not rebound to control plot levels. Although overall soil CO_2 emission decreased in the roof plots in comparison to the control during the experiment, the full extent of drought impact on CO_2 emissions may require years to determine as accumulated coarse woody debris that died as a result of drought stress needs time to decompose.

Keywords: Indonesia, ENSO, drought, soil respiration, carbon dioxide production, soil moisture

1   Introduction

The tropical forest ecosystems of Southeast Asia are currently under threat of climate change. Some climate models predict that droughts related to the El Niño Southern Oscillation (ENSO) phenomenon will increase in frequency and intensity in Indonesia and region (Sheffield and Wood, 2008, Timmermann *et al.*, 1999). Changes in precipitation regimes can alter both aboveground and belowground carbon stock allocations (Davidson *et al.*, 2004). Since tropical forest soils store one third of the global soil carbon within the top meter of soil (Jobbágy and Jackson, 2000) and much of the stored carbon has a short residence time (Amundson, 2001) changes in precipitation regimes can have rapid impact on stored carbon stocks (Trumbore *et al.*, 1995). Understanding how belowground carbon dynamics react to a changing climate is of fundamental importance to better predict the strength and direction of carbon fluxes to and from the atmosphere.

Ecosystem drought response is largely dependent on the mechanisms available to adapt to drought and the site specific soil water retention characteristics (Davidson *et al.*, 2008, Sotta *et al.*, 2007). The presence or absence of deep roots is one of the adaptation mechanisms used to mitigate drought effects (Nepstad *et al.*, 1994). There are indications that ecosystems that experience regular but strong dry seasons, such as the forests in the eastern Amazon, have adapted and developed deeper root systems to access water resources deeper in the soil profile (Nepstad *et al.*, 1994). In contrast, ecosystems that receive a high amount of rainfall and do not experience regular extended dry seasons, such as forests in Indonesia, typically have shallower root systems (Schenk and Jackson, 2002) which may therefore render them more vulnerable to droughts.

While there has already been extensive research done on drought effects in the tropical forests of Latin America (Brando *et al.*, 2008, Fisher *et al.*, 2007, Nepstad *et al.*, 2002c, Phillips *et al.*, 2009), relatively little emphasis has focused on drought vulnerabilities of tropical forests in Southeast Asia. To evaluate the drought susceptibility of Indonesia's tropical forests we established a large-scale throughfall manipulation experiment on an upland forest site on the island of Sulawesi. In this paper we report on soil carbon dioxide production dynamics measured spatially across the experiment plots, vertically within the soil profile to 2.5 meters depth. We also partitioned CO_2 production into leaf litter, belowground heterotrophic (microbial), and autotrophic (root) respiration sources. The objectives of this study were two-fold:

1. To identify how different CO_2 production sources react to drought and subsequent rewetting.

2. To identify the temporal and spatial controls regulating soil CO_2 production.

Our expectations were that this sub-montane tropical forest ecosystem will be drought sensitive. This ecosystem has rarely, if ever, experienced extended dry periods and accordingly has not adapted mechanisms to deal with drought. We hypothesize that the ecosystem would exhibit a progressive decrease in soil respiration as different CO_2 production sources begin to exhibit drought stress. The ecosystem recovery would depend highly on the severity of the drought and whether plants die due to drought stress.

2   Materials and Methods

2.1   Site description

The simulated drought experiment was carried out in a old-growth pre-montane tropical forest on the eastern edge of the Lore Lindu National Park in central Sulawesi, Indonesia (1.494°S, 120.057°E) at 1,050 meters above sea level (m.a.s.l.). The plots were established in the remote Pono Valley, a two hour walk from the village of Toro on a geomorphological terrace in an otherwise rugged and steep landscape. This site was selected because of its undisturbed condition, its well drained soils, the deep water table (>4 m) and a mild slope (0-20°), which provided good conditions for the building of the throughfall displacement roof. The forest has a high tree species diversity with about 130 species ha^{-1}, an average tree stem density of 456 stems per hectare (>10 cm DBH) and a canopy height of about 45 m (Culmsee and Pitopang, 2009).

The site's heavily weathered soil have been classified as a Ferralsol (World Reference Base for Soil Resources, Leitner and Michalzik, unpublished data), having a clay-loam texture dominated by kaolinite clay and hematite. The topsoil (top 40 cm) was acidic with a pH of 4.5 (pH (H_2O), it had a low bulk density 0.9 g cm^{-3}, and a C:N ratio of 13.3. Soil chemical and physical properties for the control and roof plot soil profiles are summarized in Table 1. Organic matter decomposition rates were rapid as was evident by the thin organic layer mat (on average 3.8 cm thick). The majority of both fine and course roots were concentrated within the top 20 cm of soil (74% and 91% respectively)(Hertel *et al.*, 2009).

Precipitation at the site, measured at a climate tower installed onsite, was 2,901 mm yr^{-1} in 2008. The mean air temperature was 20.6°C. No clear seasonal pattern in either

precipitation or air temperature was observed during the 2.5 year weather record (March 2007 - October 2009).

Table 1: Soil physical and chemical properties: bulk density, soil texture, carbon and nitrogen content, effective cation exchange capacity (ECEC) and pH (H₂O) of the 250 cm soil profile. The values are means ± 1 SE. For all variables n = 3, except bulk density n = 6.

Depth	Bulk density $(g\ cm^{-3})$	Sand (%)	Soil texture Silt (%)	Clay (%)	Carbon $(g\ kg^{-1})$	Nitrogen $(g\ kg^{-1})$	ECEC $(cmol\ kg^{-1})$	Soil pH (H_2O)
Control Plots								
-5	0.73 ± 0.05	32.3 ± 2.1	30.3 ± 2.3	37.6 ± 2.7	34.1 ± 7.0	2.8 ± 0.5	7.2 ± 0.4	4.3 ± 0.1
-10	0.86 ± 0.04	27.7 ± 2.7	31.9 ± 3.9	40.4 ± 6.1	28.7 ± 4.4	2.1 ± 0.3	5.7 ± 0.3	4.3 ± 0.0
-20	0.92 ± 0.04	27.8 ± 2.2	29.6 ± 4.2	42.6 ± 5.0	15.2 ± 1.8	1.1 ± 0.1	4.9 ± 0.2	4.7 ± 0.1
-40	1.08 ± 0.07	28.7 ± 2.7	34.5 ± 5.7	36.8 ± 4.7	13.9 ± 1.3	1.0 ± 0.1	4.5 ± 0.4	4.6 ± 0.1
-75	1.32 ± 0.02	31.8 ± 1.4	39.9 ± 4.4	28.2 ± 5.8	6.4 ± 0.3	0.4 ± 0.0	5.4 ± 0.7	4.7 ± 0.1
-150	1.34 ± 0.03	36.1 ± 1.5	49.6 ± 1.3	14.3 ± 1.7	3.5 ± 0.3	0.2 ± 0.0	6.0 ± 0.7	5.0 ± 0.1
-250	1.27 ± 0.08	36.5 ± 5.9	52.6 ± 9.0	10.9 ± 3.1	3.2 ± 0.5	0.2 ± 0.0	5.8 ± 1.2	5.2 ± 0.0
Roof Plots								
-5	0.70 ± 0.03	26.3 ± 2.9	36.1 ± 2.4	37.6 ± 1.6	29.1 ± 3.0	2.4 ± 0.2	7.0 ± 0.4	4.4 ± 0.3
-10	0.81 ± 0.02	24.6 ± 2.6	35.9 ± 1.6	39.5 ± 1.6	25.6 ± 1.8	1.9 ± 0.1	5.5 ± 0.0	4.4 ± 0.0
-20	0.92 ± 0.03	24.7 ± 2.4	38.9 ± 4.5	36.4 ± 2.9	18.8 ± 2.0	1.3 ± 0.2	5.2 ± 0.5	4.7 ± 0.2
-40	1.13 ± 0.01	26.1 ± 1.8	38.7 ± 3.6	35.3 ± 4.0	10.8 ± 0.3	0.7 ± 0.0	5.3 ± 0.2	4.6 ± 0.1
-75	1.30 ± 0.02	31.7 ± 2.8	37.9 ± 1.7	30.4 ± 4.4	6.7 ± 1.0	0.4 ± 0.1	5.6 ± 0.3	5.2 ± 0.1
-150	1.28 ± 0.02	33.7 ± 6.6	42.4 ± 5.7	23.9 ± 5.5	4.0 ± 0.4	0.2 ± 0.0	5.2 ± 0.9	5.1 ± 0.1
-250	1.25 ± 0.06	31.6 ± 8.2	52.0 ± 9.9	16.5 ± 2.2	3.0 ± 0.5	0.2 ± 0.0	6.0 ± 0.2	5.2 ± 0.1

2.2 *Experimental design*

We established the experiment in a stratified random design using six plots, each 40 x 40 m in size, spread out over an area of approximately five hectares. While three plots were left undisturbed (control), three treatment plots, hereafter called "roof plots", were used to simulate drought conditions. In the simulated drought plots we built a transparent roof below the plantation canopy to divert throughfall away from the plot. The roof consisted of transparent polyethylene plastic sheets mounted on several thousand individual bamboo frames (0.5 x 5 m) at an average height of 1.7 m above the ground. The roof was initially ± 70 % closed, and only small gaps remained around the tree stems and between some panels. In early 2008, the roof closure was further increased to approximately ± 90 % by building custom sized panels to close gaps around tree stems and odd sized openings. Runoff was diverted into a series of wooden, plastic lined gutters and channelled down-slope away from the plots. Every two weeks the leaf litter that accumulated on the roof panels was transferred back to the soil surface. Temperature, humidity and incident radiation under the panels were unaffected by the establishment of

the roof. Along the perimeter of each plot a 0.4 m trench was dug and lined with plastic so as to prevent lateral and surface water flows from entering the plots.

All measurements were made within a 'core zone' (30 x 30 m) in the plot, leaving a 5 m buffer zone along the inside of the plot boundary to avoid edge effects. Per plot one central soil pit (0.8 m width × 1.6 m length × 3.0 m depth) was dug and equipped with gas samplers, thermocouples and soil moisture probes. Three transects per plot were set up within the 'core zone' for soil CO_2 flux measurements.

Carbon dioxide respiration measurements began in early February, 2007, two and a half months prior to the roof closure in the treatment plots. These pre-treatment measurements were made to verify that control and roof plots did not exhibit any initial systematic differences. The roof was closed at the beginning of May 2007 and remained closed for 24.5 months. The roof was opened in mid May, 2009 and measurements continued for an additional four months to monitor the recovery of the ecosystem.

2.3   Measurements of soil surface CO_2 efflux

Soil surface CO_2 efflux from soil respiration was measured using the dynamic closed chamber method described by Parkinson (1981). Soil CO_2 efflux was measured every two weeks during the 31 month simulated drought experiment using a portable infrared CO_2 gas analyzer (IRGA) mounted on a backpack frame. In total, 68 field visits were made. Two measurement campaigns (field visits) were missed in August 2007 due to an equipment failure with the gas analyzer (IRGA). During each field visit CO_2 efflux was measured at 36 chamber sites spread out over the six plots. The round chamber bases (0.045 m² area, 0.15 m height) made from polyvinyl chloride (PVC) were deployed in each plot in three randomly situated transects (two chamber bases per transect). A detailed explanation of the CO_2 efflux measurements and the IRGA calibration is described in van Straaten *et al.(2010)*.

Two additional experiments were carried out to partition soil CO_2 production sources into three components: 1) leaf litter respiration 2) autotrophic (root) respiration in the top 30 cm and 3) belowground heterotrophic (microorganism) respiration. In the litter contribution experiment, we randomly selected six experiment chambers (from the drought experiment) in the control plot and installed two additional chambers directly adjacent to these 'main' chambers (<1 m away). We transferred litter from one chamber into the second chamber. The 'main' chamber was left undisturbed and used as a control. Leaf litter respiration (R_L) was calculated by subtracting the soil CO_2 efflux respired by the empty

chamber with no leaf litter from the control chamber. Measurements were conducted during 62 of the 68 field visits made for the drought experiment measurements. Six measurements were missed because of inclement weather conditions.

The partition between autotrophic (R_A) root respiration and belowground heterotrophic respiration (R_H) was determined using a root trenching technique similar to the method described by Wang and Yang (2007). In each plot, two drought experiment chamber locations were randomly selected. Next to the 'main' chamber we installed an additional second chamber, around which a 30 cm deep trench was dug, approximately 15 cm from the outside of the chamber base. This is hereafter referred to as a "trenched" chamber. The excavation cut incoming roots and with it the supply of photosynthates from plants. The trench was double lined with a heavy duty plastic and backfilled with the original soil. In total, twelve chamber pairs were installed (six in the control and six in the roof plots) in late November 2008. Prior to making the first measurements we waited for a period of four weeks to allow soil respiration to equilibrate and the dead roots some time to decompose. Soil CO_2 efflux measurements from the chamber pairs (trenched and un-trenched) were made within a period of ten minutes of another. Respiration rates were subsequently compared. The CO_2 respired from the trenched chambers theoretically constituted the "heterotrophic" component. The belowground heterotrophic respiration component was calculated by subtracting the CO_2 produced by the litter layer (as determined from the leaf litter – soil moisture relationship) from total heterotrophic respiration. Root respiration was calculated as the difference between the trenched and the un-trenched chambers.

It should be recognized however, that the trenching approach has a few known shortcomings. The heterotrophic (microbial) respiration may be overestimated because roots are still active below the trenching zone and will therefore contribute to the CO_2 flux measured in the trenched chamber. However, this error is regarded as small considering that the majority of roots are located in the top 30 cm (80% of the fine roots and 95 % of the coarse roots). Secondly, the cut roots during the trenching will decompose and in doing so will respire CO_2, which again overestimates heterotrophic respiration. Lastly, soil moisture conditions would also have been modified in the trenched region since the absence of live roots meant that there was no active water uptake.

The trenching experiment chambers were measured biweekly. In total 20 measurements were carried out between December 21, 2008 and September 9, 2009.

2.4 Root biomass

Following the completion of the infrared CO_2 gas analyzer (IRGA) field measurements in September 2009 all the CO_2 efflux chambers were excavated to a depth of 10 cm. Roots were separated from the soil, dried and then weighed to determine the root biomass. We separated the roots into three categories: fine roots (< 2 mm diameter), medium roots (between 2 mm and 10 mm diameter) and large roots (> 10 mm diameter).

2.5 Soil air CO_2 concentrations and soil moisture depth profiles

Gas samples for analyses of CO_2 concentrations were collected from one central soil pit per plot. Samples were taken on a bi-weekly basis in tandem with the soil surface respiration measurements. Gas samplers were installed horizontally into the soil profile at different depths in the soil profile (10, 20, 40, 75, 150 and 250 cm). While the 1mm inner diameter gas samplers in the top 75 cm were 1 m long, the samplers at 150 cm and 250 cm depth were 2 meters in length to avoid errors introduced by horizontal diffusion losses through the pit wall. A detailed description of the gas samplers and the gas sampling technique is described by van Straaten *et al .(2010)*. Soil CO_2 concentration samples were taken during 70 field campaigns, in tandem with the IRGA soil respiration measurements.

Gas samples were analyzed in a laboratory at Tadulako University in Palu, Sulawesi, within 72 hours after collection in the field. The CO_2 concentration of each sample was measured with a gas chromatograph (GC) (GC-11, Delsi Instruments, Suresnes, France) with a thermal conductivity detector (TCD). Sample CO_2 concentrations were calculated by comparing the integrated peak areas to that of two known standard gas concentrations (0.07 % and 3.5 %, Deuste Steininger GmbH, Mühlhausen, Germany), to make a two point calibration.

Additional to the CO_2 concentration and temperature measurements, we also measured volumetric soil water content using time domain reflectometry (TDR) sensors (Campbell CS616) in three soil pits per plot. While in the two secondary soil pits TDRs were installed at 10, 40 and 75 cm depths, TDRs in the central soil pit were installed adjacent to each gas sampler at the same respective sampler's depth. The TDR sensors were inserted horizontally into the undisturbed soil at the end of a 30 cm hole dug into the soil pit wall. Soil moisture was recorded hourly using a datalogger (Campbell CR1000). Using undisturbed soil samples we calibrated the water content measurements using the methodology described by Veldkamp & O'Brien (2000). TDR measurements began on

March 27, 2007 in the roof plots and on May 31, 2007 in the control plots. The start of the measurements was delayed resulting from a lightning strike in March 2007 that damaged both dataloggers and TDR sensors. Volumetric water content was subsequently recalculated to water matrix potential using pF curves measured using pressure plates in the laboratory at the Georg-August-University of Goettingen, Germany (van Genuchten, 1980).

2.6 *CO₂ production in soil profiles*

The vertical partitioning of CO_2 production sources within the soil profile was modeled using the methodology described by de Jong and Schappert (1972). This approach requires five assumptions: 1) gaseous diffusion is the only mechanism of CO_2 transport (no convective transport of CO_2), 2) changes in soil air CO_2 concentrations over time are very small, i.e. conditions are considered steady state, 3) there are no CO_2 sinks within the soil profile 4) horizontal or downward diffusion is considered negligible and 5) soil air pressure is at equilibrium with the soil surface.

Soil CO_2 production was determined by calculating the difference between the CO_2 flux coming in (from below) and going out (to upper layers above) for each horizontal (5 cm) layer. The CO_2 flux of each layer was determined using Fick's first law of diffusion (Equation 1). It states that the rate of gaseous diffusion is proportional to the concentration gradient in space − in our case, soil depth. The mathematical equation is expressed as follows:

$$F = -D_s \times \frac{\partial C}{\partial z}$$
(1)

where F is the CO_2 flux at any point in the soil profile (mg C m^{-2} h^{-1}); D_s is the gas diffusion coefficient of CO_2 in soil (cm² s^{-1}) and $\partial C / \partial z$ is the change in CO_2 concentration (%) with change in soil depth (cm).

The production term of each layer was calculated by adjusting Fick's second law (equation 2), which predicts how diffusion changes the concentration field with time.

$$\frac{\partial C}{\partial t} = -\frac{\partial F}{\partial z} + S$$
(2)

$\partial C / \partial t$ is the change in CO_2 concentration in time (t); $\partial F / \partial z$ is the change in CO_2 flux with depth; and S is the sink / source term, i.e. the amount produced in each layer. Based on the steady-state assumption, $\partial C / \partial t$ is equal to zero. The production equation can therefore be rearranged to solve for S. Inserting equation 1 into the rearranged equation 2 we get the following:

$$S = -\frac{\partial}{\partial z}(D_s \times \frac{\partial C}{\partial z})$$
(3)

The first step to solve this equation is to calculate the gas diffusion coefficient in soil (D_s). D_s is a fraction of the CO_2 gas diffusion in free air (D_o), which for CO_2 is 0.139 cm² s⁻¹, at 273 K and 1013 hPa pressure. Within the soil profile the diffusion coefficient is slower than it is in free air because soil particles and soil water increase the tortuousness of the gas pathway. High bulk density (low porosity) will slow gaseous diffusion. Likewise, a saturated wet soil will have much of the pore-space occupied by water which slows gaseous diffusion. Liquid phase CO_2 diffusion (in free water) is negligible as it is more than 8,000 times slower than CO_2 transport through free air (Moldrup *et al.*, 2000).

There have been a number of equations developed in the past century to predict diffusion coefficients through different soil media (Millington and Quirk, 1961, Millington and Shearer, 1971, Moldrup *et al.*, 2000, Penman, 1940, Sallam *et al.*, 1984). For the soil conditions present at this site, the Penman (1940) equation best described the diffusion coefficient:

$$\frac{Ds}{Do} = 0.66 \times a$$
(4)

where D_s is the CO_2 gas diffusion coefficient in soil (cm² s⁻¹), D_o is the CO_2 gas diffusion coefficient in free air (cm² s⁻¹), and *a* is the air filled pore-space (m⁻³ m⁻³). Soil porosity (m⁻³ m⁻³) and volumetric soil water content (m⁻³ m⁻³) were linearly interpolated for all sampling depths. The air filled pore-space is simply the volume of air still in the pore-space.

The second step to solving the production formula (equation 3) is to calculate the change in CO_2 concentration with change in depth ($\partial C / \partial z$). Here we used an approach described by Gaudinski *et al.*(2000), whereby CO_2 concentration profiles were fit with an exponential function (equation 5):

$$[CO_2]_z = CO_{2\infty}(1 - e^{-\beta z}) + 0.04 \tag{5}$$

where, $[CO_2]_z$ is CO_2 concentration (%) at soil depth z, $CO_{2\infty}$ is the asymptotic CO_2 concentration reached at an infinite depth, β is a fitted parameter, z is soil depth, and 0.04 is an adjustment factor to achieve near atmospheric CO_2 concentrations at the soil surface. When the adjusted R^2 from the exponential function was below 0.8 the soil CO_2 production calculation was not carried out for that soil pit profile for that particular date as it was felt that the calculated function was inadequate to describe the measured CO_2 values. This tended to occur when there was a build up of CO_2 just below the soil surface which typically occurred after a rain shower where the upper soil layers became saturated and created a diffusion block. This is indicative of a non-steady state condition. The first derivative of the fit function (equation 5) was calculated to determine the rate of change of CO_2 concentration with depth.

Using the calculations from the diffusion coefficient (equation 4) and the change of CO_2 concentrations with change in depth (first derivative of equation 5) we could calculate the CO_2 production for each vertical layer using equation 3. We obtained an estimate of soil surface respiration by adding the fluxes from each layer. The quality of the modelling effort was evaluated by comparing the modeled surface flux with the measured surface flux using the IRGA.

2.7 Isotope analysis

To verify the origin of the CO_2 within the soil profile $^{13}CO_2$ isotope signatures were measured. Soil air samples was taken from each of the control plots at 250 cm depth, stored in airtight, stainless steel vials and transported to the Centre for Stable Isotope Research and Analysis (KOSI, Georg-August-University of Goettingen, Germany) for analysis using a Isotope Ratio Mass Spectrometer (Finnigan MAT Delta Plus, Bremen, Germany). The isotopic signature can indicate whether the CO_2 was produced either biologically or from geological sources.

2.8   Data analysis

We divided the experiment into four time periods. The fist was the "pre-treatment period" which started on February 14, 2007 and lasted until the roof was closed on May 1, 2007 – a total of 77 days. The period of roof closure has been divided into two periods, the first being the initial nine months when the drought effect was still moderate hereafter called "treatment period #1" (from May 1, 2007 to February 1, 2008; 276 days), followed by "treatment period #2", which corresponded to the time when the drought effect was more severe and ran until May 15, 2009 when the roof was opened (470 days). The fourth was the "post-treatment period" which extended until September 10, 2009 (116 days).

Throughout the experiment, roof plot measurements were compared to adjacent control plots to compare roof plot ecosystem drought response to normal fluctuations. Individual soil CO_2 efflux chamber measurements were averaged for each plot at each measurement date and logarithmically transformed in order to normalize data distributions. The significance of the drought effect difference was tested using linear mixed effects models for the four time periods mentioned above. In the model, the desiccation treatment was considered a fixed effect while the measurement day (from day 1 to day 939) and plot were considered as random effects. Differences were considered significant if $P \leq 0.05$. Additionally, temporal autocorrelation in this time series CO_2 flux dataset was corrected for by using a first order autoregressive model.

The relationship between overall soil CO_2 efflux with soil moisture (at 10 cm depth), soil surface temperature, solar radiation, root biomass and the chamber distance from tree stem were tested using linear regressions. Non linear regressions were used to explain the heterotrophic respiration with soil moisture using an inverse parabolic function. Leaf litter respiration relationship with soil moisture was tested using an exponential function. The reported coefficient of determination (R^2) in the non-linear model was calculated in the same way as the linear model. An independent t-test was used to identify whether the difference between root biomass measurements between treatments was significant. All statistical analyses were done using the statistical package R version 2.8.1 (R Development Core Team, 2008).

3   Results

3.1   Soil moisture

Soil moisture was recorded continuously in both roof and control plots (Fig. 1b) in a total of 18 soil pits across the project area (three soil pits per plot). Due to the installation delays described earlier, no TDR measurements were made in the control plots during the pre-treatment period, and consequently there is no direct pre-treatment comparison between the control and roof plots. However, soil moisture measurements in the roof plots at 10 cm depth were within the same range as was measured in the control plots once they were installed. Shortly after roof closure, we started to measure decreases in soil moisture at the soil surface in the drought simulation plots. In these plots the soil moisture decreased during the course of the experiment. During the first nine months (treatment period #1) the soil surface in the roof plots experienced minor recharges from throughfall that entered between gaps in the roof panels. After the roof coverage was improved in early 2008 surface recharge was minimal. In January 2008, as a result of both improved roof coverage and a natural dry period, soil water contents in the roof plots dropped below permanent wilting point at 10 cm soil depth and remained below it until the roof was re-opened. At the driest point in the drought experiment in May 2009, just prior to roof opening, the volumetric water content was 0.342 m^3 m^{-3}, which is equivalent to a pF of 4.46. According to our measurements permanent wilting point was not reached below a depth of 10 cm. At deeper soil depth (150 and 250 cm respectively) the difference in soil moisture between the roof and control plots was not as pronounced. Following roof opening, soil moisture in the roof plots began to increase, however, due to the lack of sufficient rainfall in the following months the soil moisture did not return to control plot levels.

In the control plots, soil moisture remained on average wetter than field capacity and did not approach permanent wilting point at any point during the experiment. A strong natural drought was experienced between January and February 2008. The remainder of 2008 was very moist (Fig. 1c.). The onset of an El Niño Southern Oscillation phenomenon in 2009 brought drier conditions to the region, including less frequent rainfall events and as a consequence resulted in drier soil conditions.
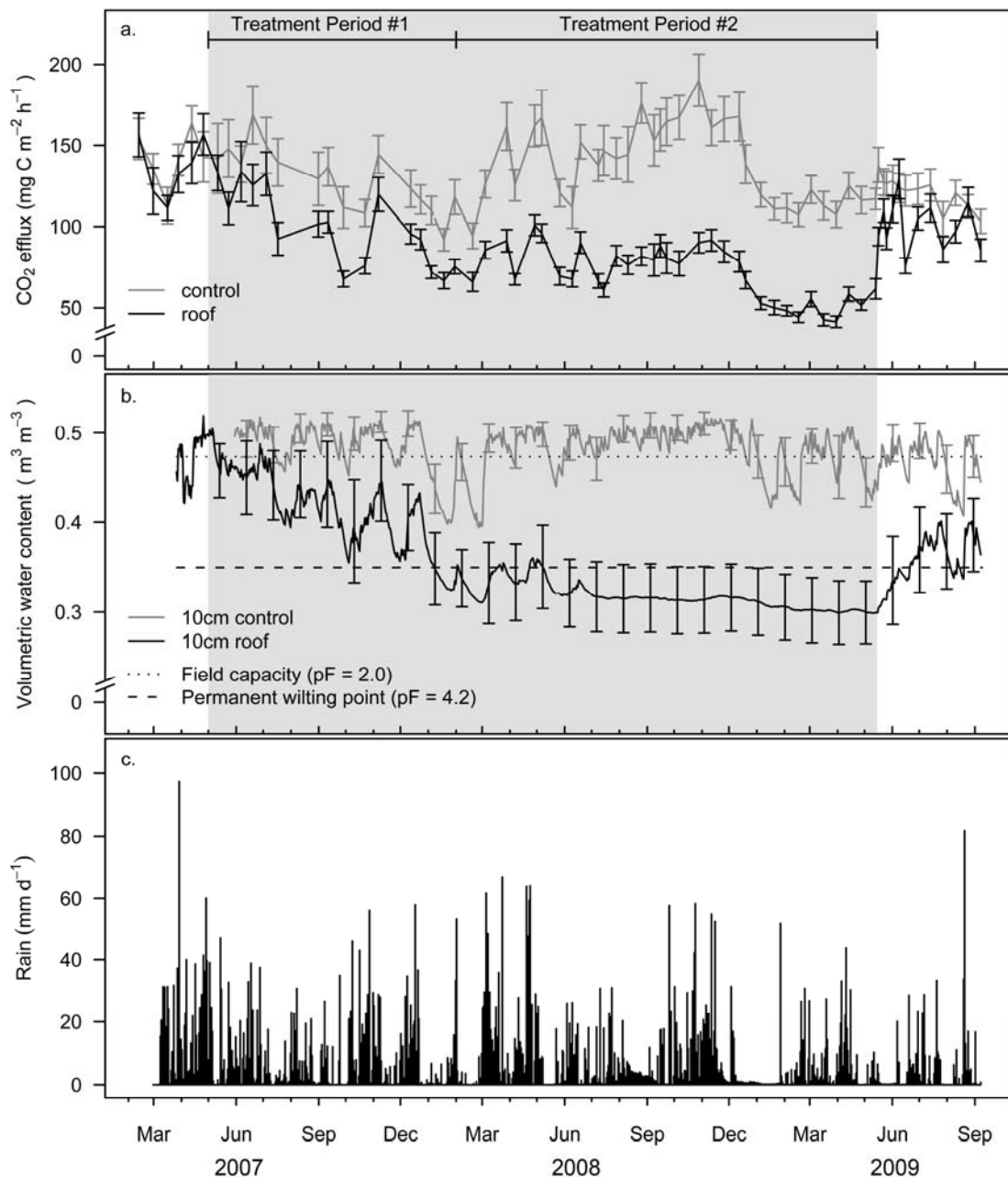
Figure 1: Soil CO$_2$ efflux, volumetric water content and daily precipitation. (a) Average soil surface CO$_2$ efflux in control and roof plots, (b) average volumetric water content (VWC) at 10cm soil depth in control and roof plots and (c) daily precipitation. Error bars indicate ±1 SE. The shaded area indicates the period of roof closure.

3.2 Air and soil temperature

During the two and a half year experiment, we did not measure a seasonal fluctuation in air temperature. Air temperatures just above the soil surface (measured using a handheld thermometer) fluctuated by a total of 7.1°C during the 31 month experiment period, ranging from a minimum of 18.5°C to a maximum of 25.6°C and averaged 22.1 ± 1.4°C (mean ± SD). Air temperature reached a daily maximum in the early afternoon between

12:00 and 14:00 (Table 3). Correspondingly, the temperature in the soil did not exhibit strong fluctuations, ranging by only 4.5°C from a minimum temperature of 19.0°C to a maximum of 23.5°C. The average soil temperature was 20.8 ± 0.8°C (mean ± SD). Daily soil temperature was highest during the late afternoon between 16:00 and 18:00 (Table 3). There was no soil temperature difference between roof and control plots. Soil temperature did not change with soil depth, although the temperature fluctuations became smaller.

3.3 Soil CO_2 efflux and environmental controls

During the six field measurement campaigns made during the pre-treatment period, soil CO_2 efflux emissions were not significantly different between control and roof plots (Table 2, Fig. 1a). Following roof closure, CO_2 effluxes in the roof plots began to decline in comparison to the control. The drought effect was not very pronounced during the first nine months, until the end of February 2008. During this first phase of the drought the difference in soil CO_2 effluxes between treatments exhibited an initial decline but levelled off at approximately 30 mg C m^{-2} h^{-1} (23 %) lower than the control. This first phase of the drought corresponds to treatment period #1. In early March 2008 the difference in soil CO_2 efflux between roof and control plots became more pronounced. During the second drought phase (treatment period #2) the difference in soil respiration was on average 67 mg C m^{-2} h^{-1} (48 % lower than the control). Soil CO_2 effluxes in the roof plots reached a minimum in late March 2009, where the average respiration rates in the roof plot decreased by 61 % compared to the control ($P < 0.01$). Over the duration the roof was closed respiration rates decreased an average of 39 % in comparison to the control. Immediately following roof opening CO_2 efflux spiked and within a one week period the roof plots were only 14 % lower than the control plots. In the 12 follow up measurements in the post treatment period, roof plot respiration rates increased but rarely surpassed control plot levels. There was only a marginal significant difference ($P = 0.07$) between the control and roof plots during this time period. Over the duration of the experiment the average annual soil respiration from the control plots was 11.7 ± 0.3 Mg C ha^{-1}, while the drought plots respired an annual average of 7.8 ± 0.3 Mg C ha^{-1}.
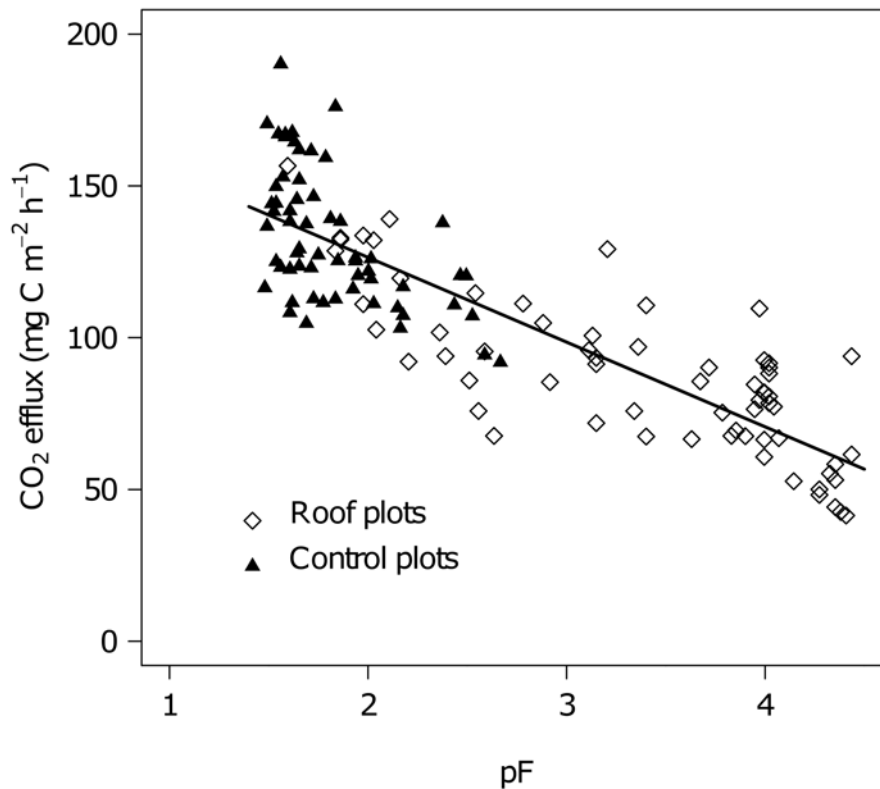
Figure 2: Relationship between soil water potential (pF) and soil CO_2 efflux (CO_2 efflux = -27.9(pF) + 182.3, R^2 = 0.72, p < 0.05, n = 126) showing the average soil CO_2 efflux measurements from roof and control plots for each measurement campaign. Each point represents the average of 18 CO_2 efflux measurements. Volumetric Soil moisture was measured using TDR sensors from three soil pits per plot embedded horizontally at 10 cm soil depth.

Soil CO_2 efflux exhibited a strong linear relationship with soil moisture (R^2 = 0.72, P < 0.01). Soil respiration rates were highest when soils were very wet and were lowest when soils were very dry (Fig. 2). No detectable relationship was measured between soil respiration and soil temperature or with solar radiation.

Additionally, no correlation was determined between soil moisture and soil temperature, nor was there a strong diurnal pattern exhibited in soil respiration during daytime hours (Table 3).

Table 2: Experiment soil surface CO_2 efflux (mg C m^{-2} h^{-1}), soil air CO_2 concentrations (%) and soil CO_2 production for 50 cm depth intervals (mg C m^{-2} h^{-1}) for different soil depths for the pre-treatment, treatment, post-treatment. Mean value ± 1 SE. n = number of sampling campaigns.

	n	Pre-treatment Control	Roof	n	Treatment period #1* Control	Roof	n	Treatment period #2** Control	Roof	n	Post-treatment Control	Roof
CO_2 efflux (mg C m^{-2} h^{-1})	6	140.4 ± 12.1	133.4 ± 12.6	16	130.5 ± 8.5	100.5 ± 6.5	34	138.4 ± 5.3	71.6 ± 2.9	12	119.3 ± 6.4	100.6 ± 5.9
Soil CO_2 concentrations (%)	6			19			33			12		
-5 cm		0.2 ± 0.1	0.2 ± 0.0		0.4 ± 0.0	0.3 ± 0.0		0.4 ± 0.0	0.3 ± 0.0		0.4 ± 0.0	0.3 ± 0.0
-10 cm		0.5 ± 0.0	0.6 ± 0.1		0.5 ± 0.0	0.5 ± 0.0		0.5 ± 0.0	0.4 ± 0.0		0.5 ± 0.0	0.5 ± 0.0
-20 cm		0.8 ± 0.0	0.7 ± 0.1		0.7 ± 0.0	0.5 ± 0.0		0.7 ± 0.0	0.4 ± 0.0		0.7 ± 0.0	0.5 ± 0.0
-40 cm		1.2 ± 0.0	1.2 ± 0.1		1.1 ± 0.0	0.8 ± 0.0		1.0 ± 0.0	0.5 ± 0.0		1.0 ± 0.0	0.7 ± 0.0
-75 cm		1.4 ± 0.1	1.5 ± 0.1		1.4 ± 0.0	1.1 ± 0.1		1.3 ± 0.0	0.8 ± 0.0		1.3 ± 0.0	1.1 ± 0.0
-150 cm		3.2 ± 0.1	2.8 ± 0.1		2.8 ± 0.1	2.3 ± 0.1		2.4 ± 0.1	1.7 ± 0.0		2.5 ± 0.0	2.2 ± 0.0
-250 cm		3.6 ± 0.1	3.5 ± 0.1		3.4 ± 0.1	3.3 ± 0.1		3.0 ± 0.1	2.6 ± 0.1		3.3 ± 0.0	3.0 ± 0.1
CO_2 Production (mg C m^{-2} h^{-1})				18			33			12		
0-50 cm		-	-		69.4 ± 3.7	60.8 ± 4.7		70.9 ± 3.8	56.0 ± 1.7		65.6 ± 2.5	83.8 ± 3.8
50-100 cm		-	-		17.8 ± 0.9	13.0 ± 1.5		17.4 ± 0.9	9.7 ± 0.4		15.8 ± 0.7	13.5 ± 1.0
100-150 cm		-	-		10.3 ± 0.3	10.7 ± 1.1		9.3 ± 0.3	5.7 ± 0.3		9.2 ± 0.3	8.4 ± 0.8
150-200 cm		-	-		5.7 ± 0.2	6.5 ± 0.4		4.6 ± 0.2	5.0 ± 0.2		4.7 ± 0.3	4.8 ± 0.2
200-250 cm		-	-		3.6 ± 0.2	4.6 ± 0.2		2.8 ± 0.1	4.4 ± 0.1		3.2 ± 0.2	3.9 ± 0.2
Total CO_2 production		-	-		106.8 ± 4.7	95.6 ± 7.4		105.1 ± 4.9	80.8 ± 2.5		98.5 ± 3.6	114.5 ± 4.9

* May 1, 2007 to January 31, 2008

** February 1, 2008 to May 15, 2009

Table 3: Diurnal soil CO$_2$ efflux, soil temperature and air temperature during daytime hours. The mean values are ± SE.

	Time	n	Roof Plot Soil CO$_2$ flux [mg C m^{-2} h^{-1}]	n	Control Plot Soil CO$_2$ flux [mg C m^{-2} h^{-1}]	Soil temperature [°C]	Air temperature [°C]
Mid morning	08:00-10:00	161	85.5 ± 3.1	155	117.9 ± 4.3	20.5 ± 0.0	20.6 ± 0.1
Late morning	10:00-12:00	423	87.5 ± 1.8	492	134.4 ± 2.5	20.7 ± 0.0	21.9 ± 0.0
Early afternoon	12:00-14:00	395	88.6 ± 2.0	389	136.8 ± 2.7	20.9 ± 0.0	22.6 ± 0.0
Mid afternoon	14:00-16:00	216	96.7 ± 3.7	174	131.2 ± 3.5	21.2 ± 0.0	22.5 ± 0.1
Late afternoon	16:00-18:00	14	91.0 ± 13.0	15	134.9 ± 12.1	21.2 ± 0.1	22.5 ± 0.1

3.4 CO$_2$ production from leaf litter

Leaf litter respiration contributed an average of 28 % of the total CO$_2$ flux (35.6 mg C m^{-2} h^{-1}) (Fig. 3). The contribution percentage was highly correlated to the moisture regime of the leaf litter layer. Leaf litter CO$_2$ respiration was highest when conditions were very wet and decreased exponentially when it became drier, finally approached an asymptote just above zero at a pF of approximately three (Fig. 5c). The litter layer contributed as much as 63 % to the total respiration when the moisture regime was wet or as little as 4 % when dry. Leaf litter respiration exhibited an exponential relationship with soil moisture sensors embedded in the ground at 10 cm depth (R^2 = 0.62, P < 0.001).
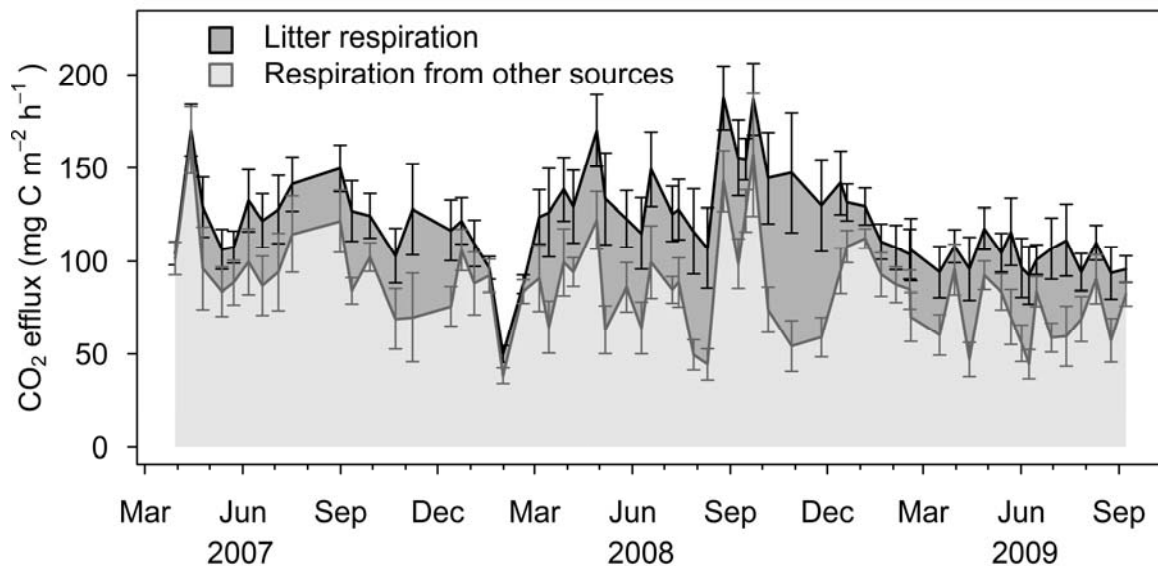

Figure 3: CO$_2$ efflux from leaf litter contribution study in the control plots. The dark grey colour indicates the CO$_2$ production derived from leaf litter, while the light grey colour denotes the CO$_2$ production from within the soil profile from other sources. The error bars indicate the standard error of the six measurements per sampling date.

3.5 *CO$_2$ production from roots and belowground heterotrophic sources*

In the control plots, roots in the upper 30 cm contributed an average of 31 % to the total soil CO_2 production. In real terms this is an average emission of 39.8 mg C m^{-2} h^{-1} (Fig. 4a). In the roof plots, the measurements made during the treatment period showed that under dry conditions CO_2 efflux from roots still contributed on average 21 % of the total soil respiration although the average emission was only 10.7 mg C m^{-2} h^{-1} (Fig. 4b). We found that autotrophic (root) respiration exhibited a linear relationship with soil moisture ($R^2 = 0.50$, $P < 0.001$) (Fig. 5a). Autotrophic respiration also showed a significant positive correlation with solar radiation ($R^2 = 0.39$, $P < 0.01$) and a negative correlation with soil temperature ($R^2 = 0.33$, $P < 0.01$).
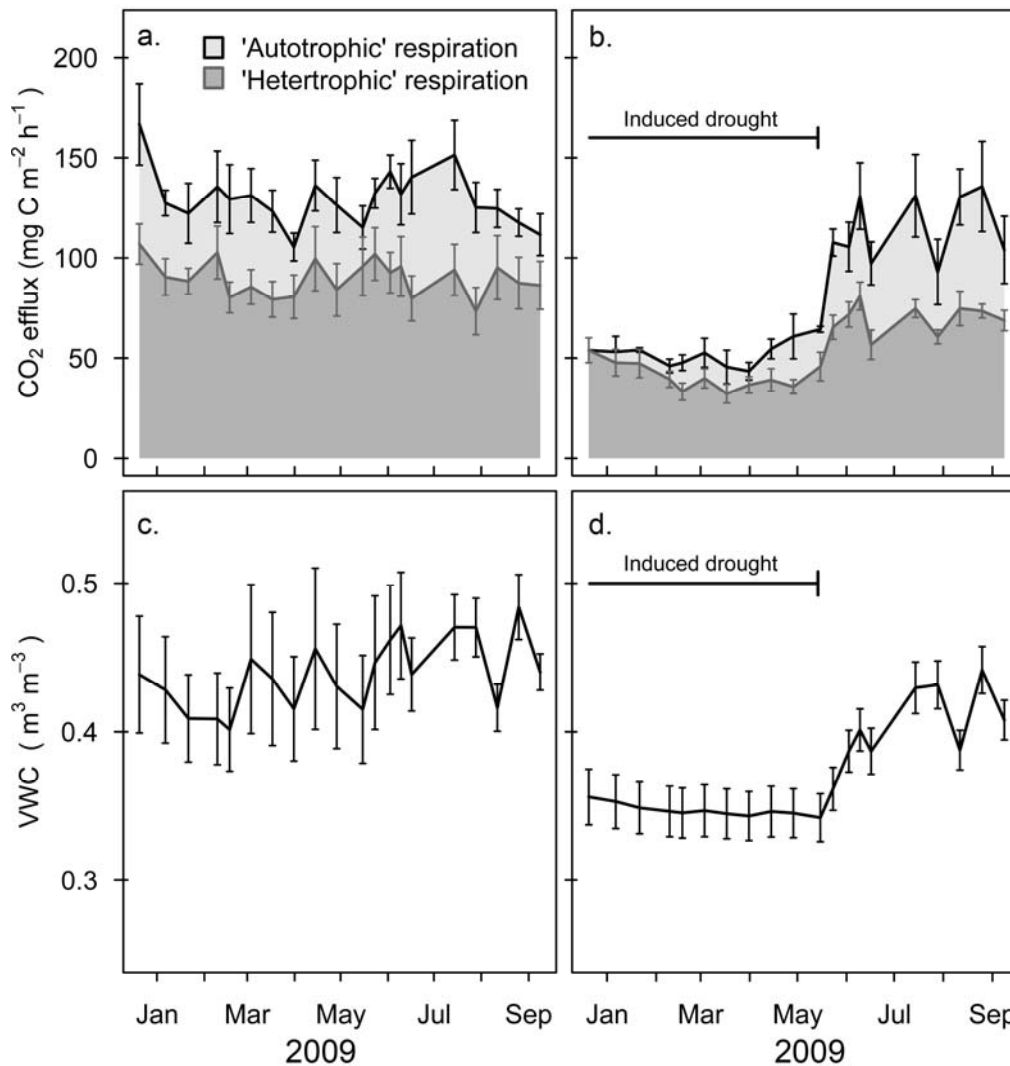

Figure 4: Heterotrophic and autotrophic respiration from (a) control and (b) roof plots as determined from the root exclusion experiment; and the respective volumetric water contents (VWC) in the (c) control and (d) roof plots. Error bars indicate ±1 SE.

Below-ground heterotrophic respiration constituted the largest CO_2 production source. In the moist control plots the contribution was on average 41% of the total CO_2 flux, which in real terms is an average emission of 52.9 mg C m^{-2} h^{-1}. However, in drier conditions under the roof, the belowground heterotrophic respiration increased proportionally relative to the total flux (on average 79 % during the most intense period of the drought), although the actual heterotrophic flux decreased (to 40.5 mg C m^{-2} h^{-1}). Heterotrophic respiration showed an inverse parabolic relationship with soil moisture; where respiration peaked at approximately field capacity and declined under both wetter and drier conditions ($R^2 = 0.82$, $P < 0.001$) (Fig. 5b). There was no correlation between belowground heterotrophic respiration and soil temperature.
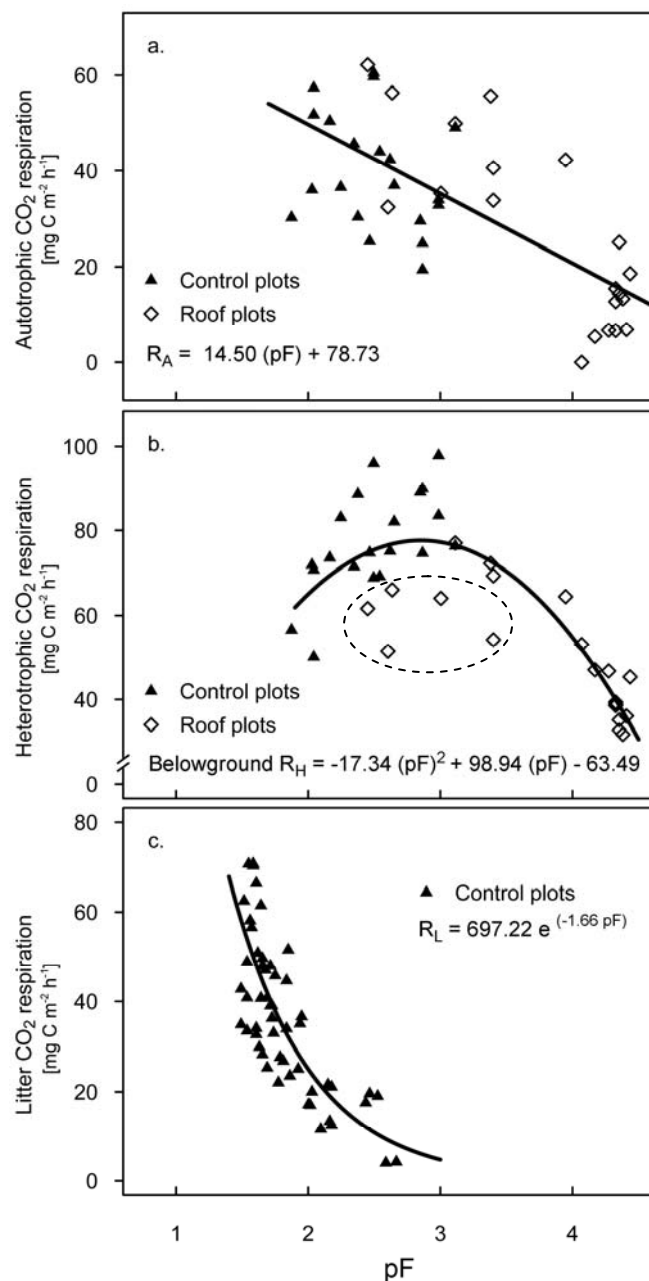

Figure 5: Relationship between soil moisture (at 10 cm soil depth) and (a) autotrophic (R_A), (b) belowground heterotrophic (R_H) and (c) leaf litter respiration (R_L). The points within the dotted ellipse shown in (b) indicate a possible hysteresis effect after rewetting.

3.6   Root biomass

The chamber-base root excavation exercise done four months following the roof opening showed that biomass in the roof plots was on average slightly lower (1.7 ± 0.2 g L^{-1}, n = 18, (mean $\pm$ SE)) than the control plot (2.0 ± 0.1 g L^{-1} n = 18, (mean $\pm$ SE)). The difference was however not significant (P = 0.11). During the root excavation exercise it was visually noted that the roof plots had many more dead roots than the control.

A strong correlation was exhibited between fine root biomass and soil CO_2 efflux in both roof ($R^2 = 0.36$, P < 0.01) and control plots ($R^2 = 0.32$, P = 0.02). Slightly weaker relationships were found in the roof plots between soil CO_2 efflux and medium ($R^2 = 0.31$, P = 0.01) and coarse roots ($R^2 = 0.20$, P = 0.06), while in the control plots no relationship was evident with the coarser root diameters. The fine root biomass exhibited a negative relationship with the average soil moisture measured at the CO_2 chambers sites (in the control plots) during the last four months of the experiment ($R^2 = 0.29$, P < 0.05).

3.7   Distance to tree stems

There was no measurable effect between soil CO_2 efflux and the distance of the chamber from the surrounding tree stems, or with the dimensions of those trees (diameter or height). We also did not find any relationship between the chambers' root biomass (fine, medium or coarse) and the respective distance to surrounding trees – indicating that root biomass was not necessarily concentrated at the base of the tree stems.

3.8   Soil CO_2 concentrations

Soil gas CO_2 concentrations from different depths in the soil profile from roof and control plots are compared in Figure 6 and in Table 2. For the control plot average we included data from only two of the three control soil pits. We excluded the data from the soil pit in plot four because the pit's location along a drainage pathway resulted in almost constant water saturation which in turn resulted in a high build up of CO_2 concentrations just below the soil surface. In general, soil CO_2 concentrations showed an exponential increase with soil depth: CO_2 concentrations were low near the surface and increased quickly with depth, before finally reaching equilibrium at a depth between 150 and 250 cm.
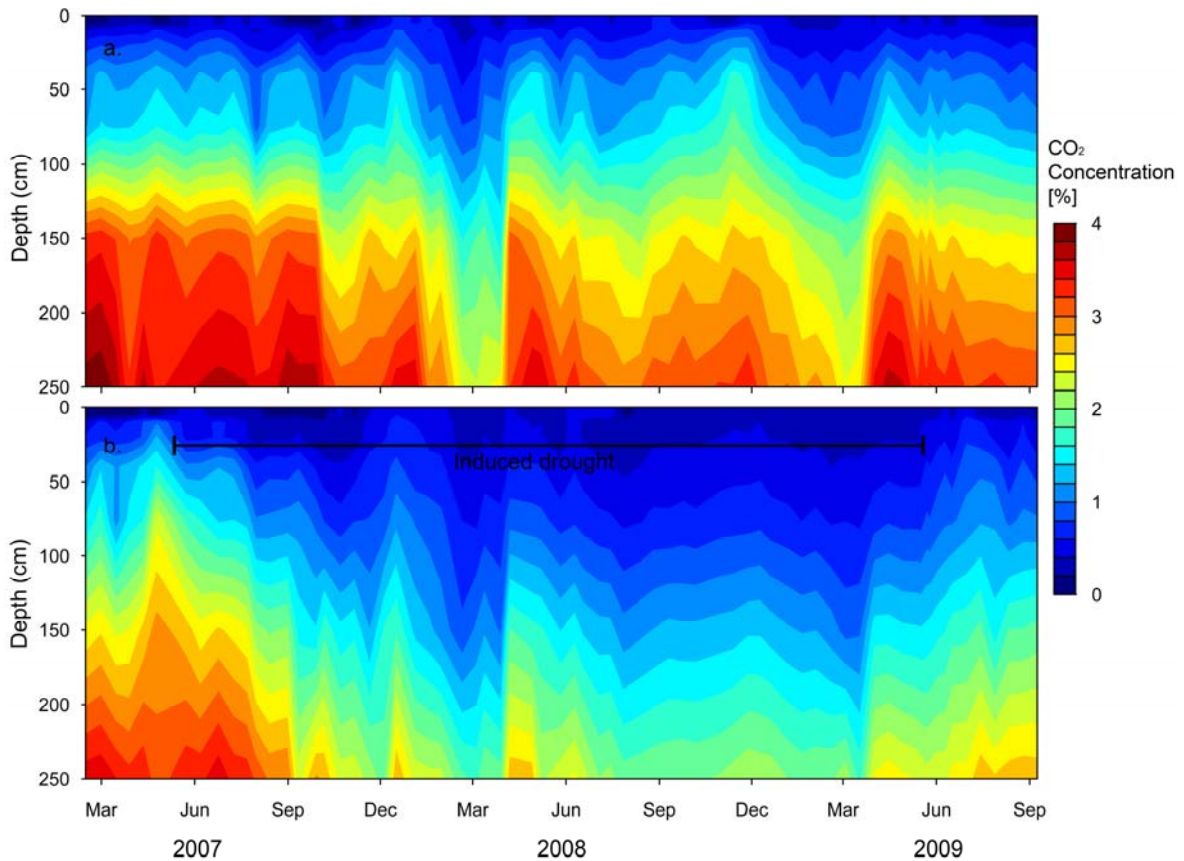
Figure 6: Soil gas CO$_2$ concentrations in the soil profile: Isopleths indicating the average CO$_2$ concentrations (percent) of (a) control plots and (b) roof plots in soil air throughout the period of the experiment.

Pre-treatment CO$_2$ concentrations were comparable at all soil depths, apart from 150 cm where the control plot average was slightly higher. The onset of the induced drought in the roof plots resulted in the degassing of CO$_2$ leading to a gradual but steady decline in CO$_2$ concentrations in the soil profile at all depth. The strongest proportional decrease to the control plot was found between 20 and 40 cm depth. Here, the roof CO$_2$ concentrations were on average 45 % lower than in the control for the treatment period. At the lowest point during the latter part of the experiment CO$_2$ concentration was 68 % lower. Upon roof opening post-treatment CO$_2$ concentrations increased in the roof plots but failed to return to control plot levels during the following four months period. During two natural droughts, one in early 2008 and a second in early 2009, we also measured a similar degassing phenomenon in the control plots which was evident at all depths.

The δC^{13} isotope signature of the three CO$_2$ gas samples taken at 250 cm depth was -23.5 $\pm$ 0.3 ‰ (mean $\pm$ SD) indicating that the CO$_2$ present in the soil profile is biologically produced.
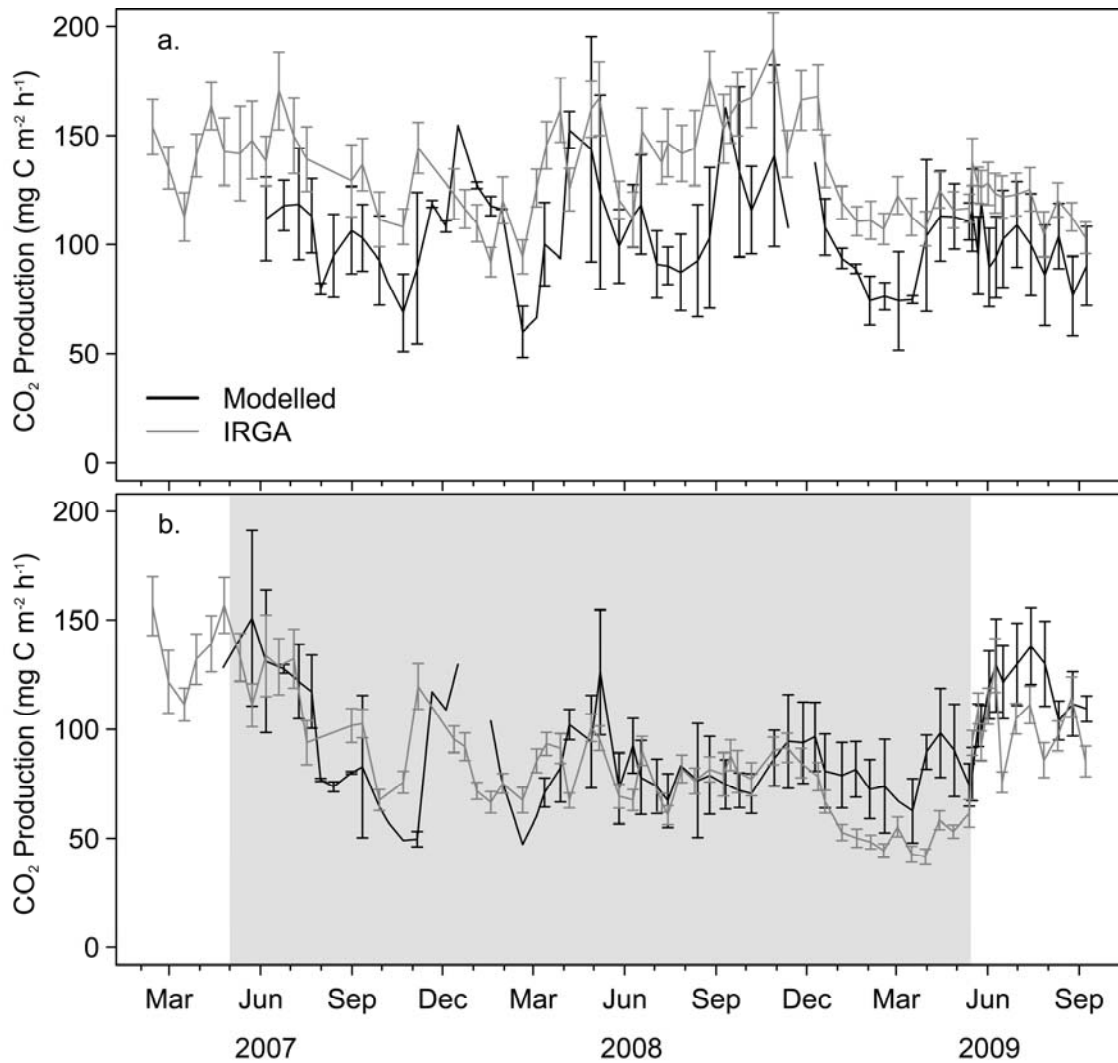
Figure 7: Comparison between modeled CO_2 production and surface CO_2 efflux measured with the infrared gas analyzer (IRGA) in (a) the control and (b) the roof plots. Error bars indicate ±1 SE. Missing average modelled values or error bars were due to non-steady conditions that followed rainfall events affecting the soil CO_2 concentration profile, which were subsequently excluded from the production calculation in one or all three soil pits. The shaded area indicates the period of roof closure.

3.9 Vertical soil CO_2 dynamics

Soil surface CO_2 respiration measurements were compared to the modeled CO_2 production (from the entire soil profile for each measurement date) to evaluate the accuracy of the modelling process in terms of: (1) the correlation coefficient between these two independent production estimates and (2) to see whether the model could predict the correct magnitude of CO_2 production. In the control plots, the CO_2 production model estimate of 104.3 mg C m^{-2} h^{-1} was approximately 22 % lower than the measured IRGA CO_2 efflux (Fig. 7a). This underestimation is likely due to the fact that the CO_2 production model does not consider leaf litter respiration. In the roof plots the difference between

modeled and control was minimal where the modeled production estimate was 5 % higher than the measured surface CO_2 respiration (Fig. 7b). Unlike in the control plots leaf litter respiration was negligible in the dry roof plots. The modelling approach showed a significant correlation with the surface IRGA measurements (control plot, $R^2 = 0.23$, $P < 0.001$; roof plot, $R^2 = 0.37$, $P < 0.001$).

During the course of the induced drought we modeled soil CO_2 production down to 250 cm depth (Fig. 8). CO_2 production was concentrated in the top layer of soil. In the control plots, the top 50 cm produced on average 67 % of the total CO_2 (averaged over the duration of the experiment). CO_2 production exhibited an exponential decrease with soil depth; it was highest just below the soil surface and approached zero production at around 175 cm depth.
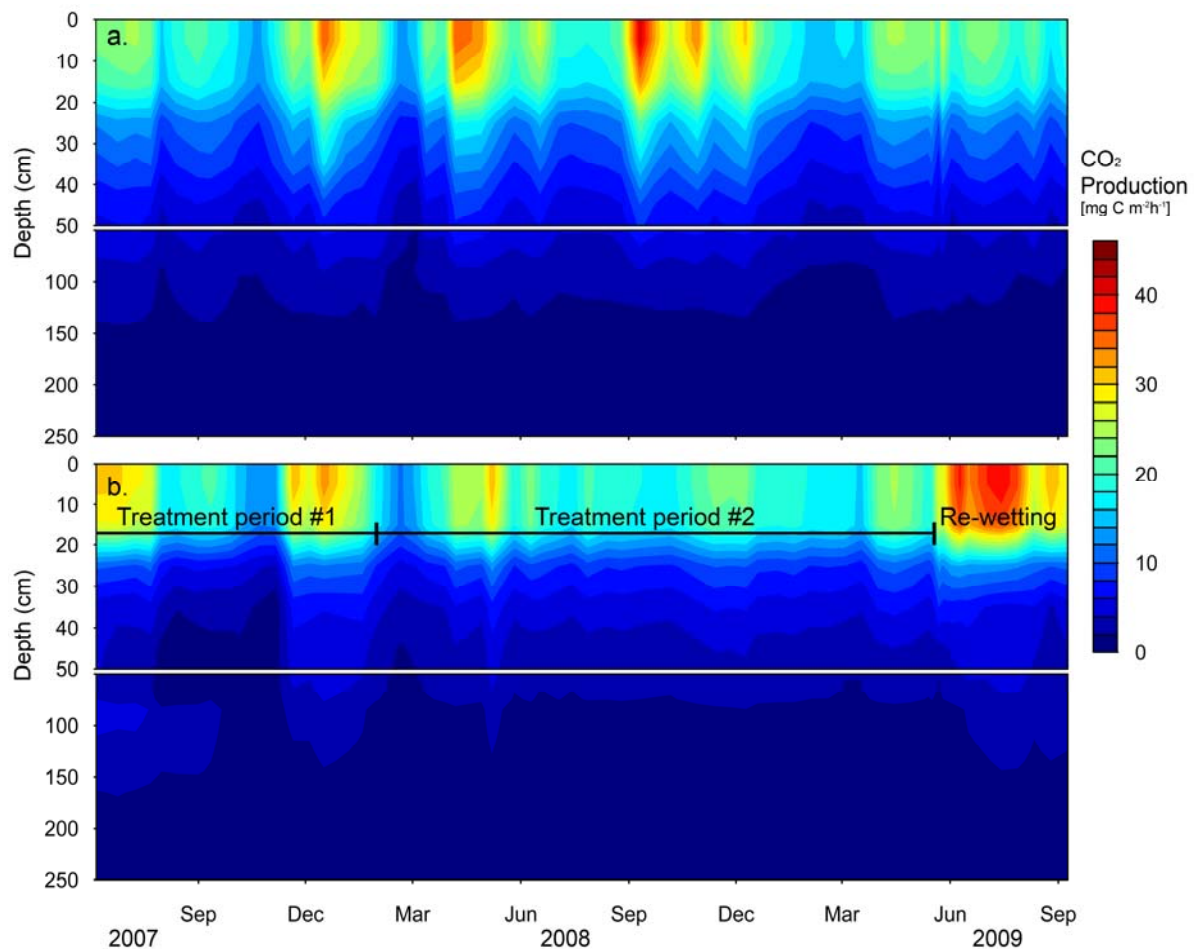

Figure 8: Soil CO_2 production in the soil profile: isopleths of average soil CO_2 production of (a) control plots and (b) roof plots throughout the experiment period.
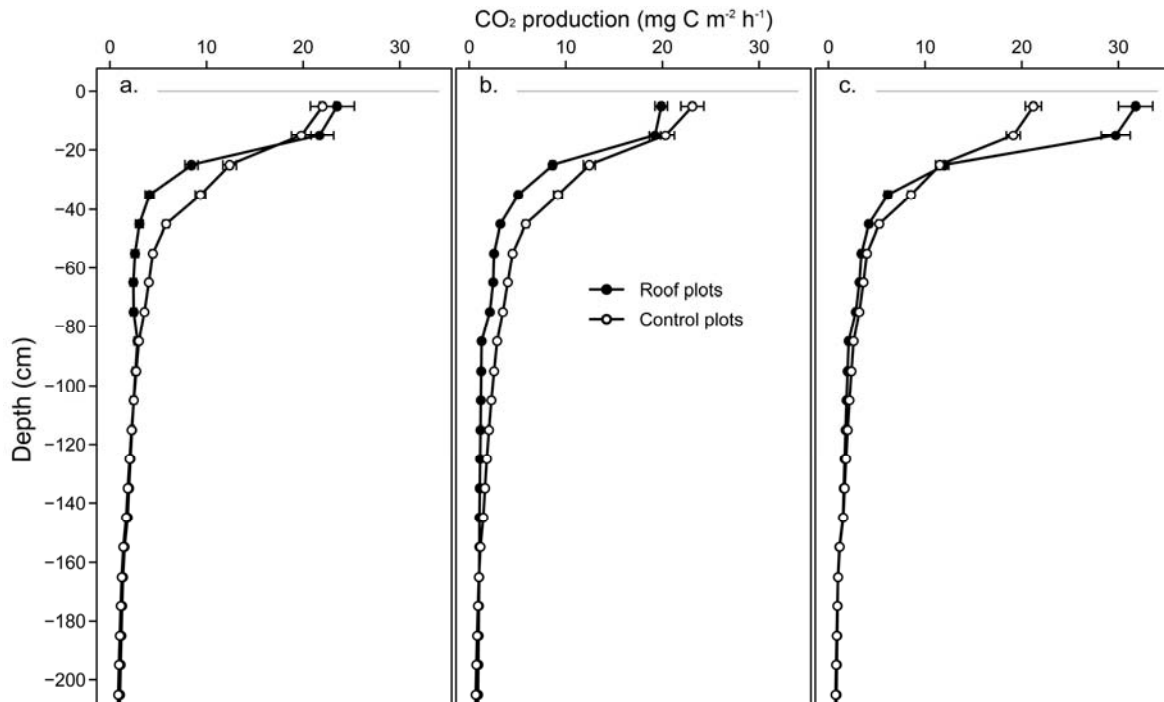
Figure 9: Vertical CO_2 production profile comparisons at 10 cm depth intervals between control and roof plots for (a) treatment period #1, (b) treatment period #2, (c) post-treatment period. Error bars indicate ±1 SE.

Roof plot CO_2 production was compared to the adjacent control plot so as to highlight changes occurring during the course of the induced drought. Comparisons for the different time periods are shown graphically in Fig. 9 and in numerical format in Table 2. Unfortunately, pre-treatment comparisons were not possible because CO_2 production was not calculated in the control plots during this time due to the delays in installing the TDR sensors; soil moisture being a required data input to calculate diffusivity. During the first nine months of the induced drought (treatment period #1) we measured a gradual CO_2 production decrease in the roof plots with the exception of a short rebound measured in November - December 2007, which was likely due to a minor rewetting event. Within the soil profile, when we compare the roof to the control plot profile, CO_2 production increased slightly in the top 20 cm, then decreased between 20 and 70 cm and below 70 cm did not change (Fig. 9a). During the second drought monitoring period (treatment period #2), the overall CO_2 production in the roof plot profiles remained relatively unchanged maintaining an average of 80.8 mg C m^2 h^{-1}. Unlike the CO_2 efflux surface measurements, the modeled CO_2 production did not detect the production drop in the first half of 2009, when the IRGA measured the strongest drought effect (Fig. 7b). In comparison to the control plots, CO_2 production in roof plots was lower at all depth during the treatment period #2 (down to 160 cm) (Fig. 9b). During the post treatment period CO_2 production

increased dramatically in the top 20 cm and surpassed control plot levels. Below 20 cm CO_2 production rose but stabilized at control plot levels (Fig. 9c).

4   Discussions

4.1   Environmental controls regulating soil CO_2 production

Soil CO_2 production in the Pono pre-montane tropical rainforest was comparable to soil respiration rates found in tropical rainforests in Asia (Adachi *et al.*, 2009, Ohashi *et al.*, 2008) and in Latin America (Davidson *et al.*, 2008, Davidson *et al.*, 2000, Schwendenmann *et al.*, 2003, Sotta *et al.*, 2006). Like in other studies, soil respiration exhibited high variability both temporally and spatially.

In this ecosystem, soil CO_2 efflux was primarily controlled by soil moisture. Soil CO_2 efflux was found to exhibit a positive linear relationship with soil matric potential (Fig. 2), where respiration was highest under moist conditions (low pF) and low under dry conditions (high pF). This linear relationship contrasts with other studies where there was an optimal for soil respiration at intermediate water contents (Davidson *et al.*, 2000, Schwendenmann *et al.*, 2003, Sotta *et al.*, 2006, van Straaten *et al.*, 2010). In our study, soil CO_2 efflux did not decrease when conditions became very wet, but instead continued to increase. Upon further investigation, we discovered that respiration from the leaf litter, belowground heterotrophic and from autotrophic sources each exhibited different responses to moisture conditions (Fig. 5). Leaf litter, for example, exhibited an exponential response to moisture regime: respiration was highest when conditions were extremely wet but decreased rapidly under slightly drier conditions and reached a near zero respiration rate at intermediate moisture levels (Fig. 5c). Of the three CO_2 production sources, the leaf litter layer was the most sensitive to moisture regime changes given its rapid decrease or increase under even moderate soil moisture changes.

Belowground heterotrophic respiration, as determined in the root contribution study and adjusted to remove the leaf litter component mathematically, was found to exhibit an inverse parabolic relationship with soil moisture (Fig. 5b). Respiration rates were highest at approximately field capacity and decreased under both dry and very wet moisture conditions. The decrease exhibited under wet conditions was likely caused by an oxygen diffusion block in the soil profile which created an anaerobic environment that was not conducive to bacterial and fungal activity (Luo and Zhou, 2006). At the dry end of the moisture gradient, heterotrophic respiration decreased due to soil microorganism drought

stress. It has been reported that bacterial activity decreases sharply between pF 2.7 and 3.5 and becomes negligible at a the permanent wilting point, below pF 4.2 (Wong and Griffin, 1976). Soil fungi on the other hand, can remain active to a pF of 4.2 because of their ability to extend hyphae across air-filled pore spaces. Under extremely dry conditions soil microorganisms may become dormant, produce spores and/or dehydrate (Schjønning *et al.*, 2003, Stark and Firestone, 1995).

Autotrophic (root) respiration exhibited a linear relationship with soil moisture (Fig 5a): it was low during dry conditions and high when conditions were wet. Finally, when we combine the three different CO_2 production source reactions to soil moisture (as described above) we can explain the linear relationship illustrated in Fig. 2.

Overall soil CO_2 respiration did not exhibit a significant relationship with either soil temperature or solar radiation. In contrast to other soil respiration studies conducted in the tropics where soil temperature was an important controlling variable for soil respiration (Ohashi *et al.*, 2008, Davidson *et al.*, 2000), overall soil respiration in this ecosystem was unaffected by soil temperature changes. This is however not surprising because the temperature fluctuations at the site were only 4.5°C over the length of the 2.5 year experiment. Of the three CO_2 production sources, autotrophic respiration showed a mild but significant relationship to soil temperature. Unexpectedly however, the relationship was negative, meaning higher soil temperatures had a negative influence on autotrophic respiration. The temperature effect may be due to physiological processes which vegetation undergoes when soils get warmer. Unfortunately, we could not corroborate this relationship without additional data or analyses.

The expression of photosynthesis on root respiration was apparent when solar radiation increases correspondingly resulted root respiration increases. Similar trends have also been observed by Wofsy *et al.* (1988), Schwendenmann *et al.* (2003) and Tang *et al. (2005).*

4.2   Spatial, vertical and temporal CO_2 production

Although soil CO_2 production exhibited a high variability across the plot, we did not identify a spatial pattern or identify potential controlling variables. Unlike a similar study done in a nearby cacao agroforestry plantation (van Straaten *et al.*, 2010), the distance of the CO_2 efflux chamber was from the adjacent tree stems had no influence on the respired soil CO_2 efflux, nor were the dimensions (DBH or height) of those adjacent trees relevant. This is not surprising however since even root biomass, which is a good predictor variable

for autotrophic respiration, did not exhibit a relationship with either distance-to-stem or with tree size.

When we examined the spatial distribution of fine roots across the control plots, we determined that roots actively influenced soil moisture conditions. Areas with the highest root biomass were also found to be the driest. Even though fine root biomass showed a significant positive correlation with soil CO_2 efflux, other sources such as leaf litter and belowground microorganisms likely masked the spatial effect that the root mat heterogeneity had on overall CO_2 efflux.

Vertically, within the soil profile, CO_2 production was highest near the soil surface and decreased exponentially with depth (Fig. 9). CO_2 production was highest in the top soil layer because most fine and course roots biomass grew in this layer (Hertel *et al.*, 2009) and most organic substrate was available in the top soil layer for heterotrophic (microorganism) decomposition.

The lack of a clear seasonal pattern in soil CO_2 efflux is not particularly surprising since there is also no clear regular annual trend in either precipitation or in temperature at this site. Similarly, the diurnal soil CO_2 efflux trends were not very pronounced and showed only a slightly elevated respiration rate in the early afternoon (Table 3).

During the 2.5 year experiment, soil CO_2 effluxes in the control plot appeared to have been strongly influenced by precipitation frequency and intensity. For example, CO_2 respiration rates were highest during the latter half of 2008, during a period of frequent rain showers where soil conditions remained near saturation (Fig. 1). When precipitation frequency and intensity decreased in early 2009 (data not shown), the soil moisture decreased, and as a result soil CO_2 efflux also declined.

4.3   Ecosystem drought response

In contrast to two drought simulation experiments conducted in tropical forests in Brazil (Davidson *et al.*, 2008, Sotta *et al.*, 2007), we measured a strong decrease in soil CO_2 efflux and production caused by the induced drought. However, before exploring the different drought adaptation mechanisms in tropical forest ecosystems, or the lack thereof, we will first examine the drought response exhibited in this forest.

Prior to the roof closure soil CO_2 production from control and roof plots were comparable (Fig. 1a and Table 2). We therefore assume that differences following roof closure are due to the induced drought effects. We observed a two-phase drought response in terms of soil CO_2 production. The first phase lasted nine months and began when the

roof was closed. During this first phase CO_2 efflux decreased by approximately 30 mg C m^{-2} h^{-1} in comparison to the adjacent control plots. The decrease occurred within a two months period and then levelled off, maintaining approximately the same difference between the two treatments. The drier conditions found under the roof likely induced a number of near simultaneous drought responses by the different CO_2 production sources. First and most importantly, leaf litter respiration decreased under the induced drought conditions. Given the sensitivity to even moderate drying (Fig 5c) it is highly likely that leaf litter layer was the main cause of reduced CO_2 production during this first drought phase. Nevertheless, belowground other drought response reactions were also taking place as is evident from results of the vertical CO_2 production modelling (Fig. 8b and 9a). While soil CO_2 production in the upper 20 cm layer remained unchanged or even slightly increased, the reductions in CO_2 production between the depth of 30 and 70 cm is thought to be due to microorganism experiencing drought stress and perhaps also due to minor shifts in rooting activity towards the surface. It is speculated that the overall magnitude of autotrophic respiration remained unaffected as tree sap flux densities remained comparable with the control (Schuldt, unpublished data) and the herb and shrub layer still appeared healthy.

In early 2008, the onset of a short but intense natural dry spell combined with the improved roof closure drove the soil matric potential below the permanent wilting point (pF 4.2) at 10 cm depth. This triggered a series of additional ecosystem drought reactions. During this second and more severe phase of the drought simulation experiment which lasted 15.5 months (treatment period #2) soil CO_2 production declined dramatically: on average 67 mg C m^{-2} h^{-1} less than emitted from the control. Leaf litter CO_2 production likely remained negligible or even increased slightly as leaf litter fall remained unchanged (Schuldt, unpublished data) and would have begun to accumulate increasing the substrate available for decomposition. But unlike the litter layer, more dramatic changes took place belowground. In contrast to the first treatment period, soil CO_2 production decreased at all depths in comparison to the control as determined using the soil CO_2 production model (Fig 9b). During this simulated drought period both autotrophic and belowground heterotrophic sources showed evidence of drought stress.

Root respiration decreased both because the herb / shrub layer had been severely effected by the drought stress, and also from trees which showed drought stress symptoms in reduced sap flux (Schuldt, unpublished data) and a decrease in stem diameter growth (Moser, unpublished data). In the root excavation exercise that followed the experiment,

we found that though not significant (perhaps because of root re-colonization within the four month rewetting period), root biomass was lower in the roof plots than in the control plots. We also noted that there were visually more dead roots in the roof plots indicating that the drought was strong enough to invoke substantial root mortality. Contrary to the deep rooted drought response mechanisms found in the Amazonian basin by Nepstad *et al.* (1994), we found no evidence to suggest that rooting activity shifted to deeper depth levels in order to find water resources. Firstly, a root biomass comparison between the control and roof plots following roof opening did not find drought induced changes at any depth within the soil profile (Moser, unpublished data). Secondly, our own CO_2 production model results did not reveal any positive production shift to greater soil depths, which could have been indicative of increased rooting activity. It should be recognized however that this modelling approach, where an exponential function is fit through the CO_2 concentrations (Eq. 5), may have the disadvantage that it smoothes out valid CO_2 production shifts.

As explained earlier, belowground heterotrophic respiration decreased as the soil dried out. Of the three CO_2 production sources, belowground heterotrophic respiration was the most resilient to drought conditions. During the last and most severe part of the drought experiment, decomposition of organic matter by microorganisms was responsible for producing on average 79 % of the total CO_2 respired (Fig. 4). We speculate that the high contribution coming from heterotrophic respiration could have two possible explanations. First, it may be caused by a methodological bias inherent of the root trenching methodology where heterotrophic respiration estimates are generally overestimated. The details of the shortcomings are described briefly in the Materials and Method section. Secondly, drought induced root mortality will have increased the substrate availability for microorganism decomposition. And, even though conditions were not optimal the increased labile carbon substrate in the soil provided a larger surface area available for microbial activity.

4.4 Ecosystem rewetting

When the roof was opened in May 2009 and throughfall began to rewet the soil, the ecosystem began to recuperate. Both soil surface CO_2 efflux and the vertical CO_2 production model measured a sharp increase in soil CO_2 production immediately following the roof opening, although the CO_2 surface efflux measurements using the IRGA rarely surpassed the control during the rewetting phase (Fig. 1a). It is suspected that the initial

rewetting caused some of the labile carbon stocks that had accumulated during the drought (both above and below ground) to mineralize. Surprisingly however, belowground autotrophic respiration in the roof plots did not return to control plot levels. We suspect this is due to a possible hysteresis effect where soil microbiological communities were still in the process of re-colonizing and recuperating after the drought (the points found circled in Fig 5b). Similar findings have also been reported in other ecosystems that experienced drought and rewetting cycles (Acuña *et al.*, 2005, Strack and Price, 2009).

Root respiration recuperated to control plot levels despite the severe dieback experienced by the herb and shrub layer (Fig 4b), suggesting there was active tree root activity to compensate for decreased root respiration from the understory vegetation. It is speculated that overall soil CO_2 efflux did not return to control plot levels during this time because both the understory vegetation and belowground microbial populations were still in the process of recovering. Although the CO_2 production model incorrectly overestimated overall CO_2 production (as is apparent in Fig. 7b), the model results still highlight that that production increased dramatically at the soil surface (Fig. 8) while below a depth of 20 cm the CO_2 production returned to near control plot levels (Fig. 9c).

4.5 *Modelling of soil CO_2 production*

The discrepancy observed in the control plots (Fig. 7a) between the vertical CO_2 production model and the IRGA surface measurements is due to the fact that the production model does not consider CO_2 produced by the leaf litter layer. As mentioned earlier, leaf litter contributes on average 28 % of the total CO_2 production (Fig. 3). In the roof plots this difference was not observed as leaf litter respiration was negligible under the dry conditions. Furthermore, the overestimation of emissions from the CO_2 production model during the last year of the experiment (Fig. 7b) is attributed to one soil pit which had higher than average CO_2 production.

Both the significant correlation between the modeled CO_2 production and the IRGA surface measurements (control, $R^2 = 0.23$ and roof, $R^2 = 0.38$), as well as the fact that the modeled results were within the same range measured using the IRGA validates the use of the Penman (1940) diffusion coefficient equation in the production model used in this study. Model results obtained by using the diffusion coefficient equations developed for non-aggregated soils by Millington and Shearer (1971), for aggregated soils by Millington and Quirk (1961) and for undisturbed soils by Moldrup *et al.* (2000) produced results that did not correlate with soil surface emissions and was not of a comparable order of

magnitude with the CO_2 production measured by the IRGA. This validation illustrates that the Penman (1940) equation best described the soil medium's gas diffusion properties.

Although the two independent methods (IRGA and CO_2 production model) were significantly correlated the relationship was still not perfect. It is expected that since these two methods of calculating total CO_2 production were not made from the same physical location the differences exhibited are likely due to the innate high spatial variability exhibited by soil CO_2 production and the lack of enough soil pit replicates.

4.6   Drought response comparison

The differences observed in drought response of soil CO_2 production between this study and two similar drought simulation experiments conducted in the Amazon The differences observed in drought response of soil CO_2 production between this study and two similar drought simulation experiments conducted in the Amazon (Davidson *et al.*, 2008, Davidson *et al.*, 2004, Sotta *et al.*, 2007) highlights a spectrum of drought adaptation mechanisms in tropical forest ecosystems. At one extreme, the throughfall displacement experiment by Davidson *et al.* (2008, 2004) in the Tapajós National Forest, Brazil on an Oxisol, showed little effect to the ecosystem and on soil surface CO_2 fluxes. The experiment by Sotta *et al.* (2007) in the Caxuianã National Forest, Brazil exhibited a moderate three phase CO_2 production drought response. And at the other extreme, the experiment described here had a strong drought response.

As Nepstad *et al.* (2002a), Sotta *et al.* (2007), and Davidson *et al.* (2008) each point out, tree rooting depth is an important drought adaptation mechanism. Unlike the two Amazonian roof experiment sites where rooting architecture was in general much deeper (> 10 m at Tapajós and up to 5 m at Caxuianã), trees in the ecosystem at the Pono site were not very deep rooted (max. fine root depth: 2.8 m; max. coarse root depth: < 1 m (Hertel *et al.*, 2009)). Accordingly, given the lack of established deep roots and the sluggish root redistribution (if any) at the Pono site, the only evident drought response mechanism used here was a passive reaction - waiting for rain.

It is speculated that the lack of a pronounced dry season and the high amount of precipitation in this region of central Sulawesi, Indonesia, meant that forests did not have to adapt mechanisms such as deeper roots to mitigate drought effects. A review paper by Schenk and Jackson (2002) substantiates this generalization, as they found a positive correlation between the length of the dry season and rooting depth in tropical forests and secondly found a negative correlation between annual precipitation and rooting depth

When we consider soil texture differences and the influence on soil water retention properties, the soil at the Pono site (clay-loam) was somewhere between that of the two other drought experiments (60-80 % clay at Tapajós and 70-95 % sand at Caxuianã in Brazil). The severity of the drought effect measured at the Pono site in comparison to the two other sites was therefore likely not caused by the soil water holding capacity differences but by other ecosystem drought adaptation.

5 Conclusions

The strong decrease in soil CO_2 efflux measured during the simulated drought and the subsequent weak rebound measured thereafter during the rewetting phase meant that the overall soil CO_2 respired from the roof plots during the 31 month experiment was lower than the adjacent control. The reduced soil CO_2 production illustrates how sensitive belowground carbon dynamics in this ecosystem are to drought. The simulated drought not only caused a slow-down in litter and soil organic matter decomposition, but perhaps more concerning for ecosystem health, the drought was severe enough to cause strong root respiration declines.

CHAPTER 4

SYNTHESIS

1 Drought effects on soil CO_2 production

The effects of climate change on hydrological cycles, such as increased frequency and intensities of droughts or changes in precipitation patterns, will have direct consequences on terrestrial carbon stock dynamics (Clark, 2004, Davidson *et al.*, 2008, Heimann and Reichstein, 2008, Nepstad *et al.*, 2002c). Since tropical soils are recognized as a major carbon repository with short residence times (Amundson, 2001, Jobbágy and Jackson, 2000), it is imperative to understand how outside influences such as changes in soil moisture (because of changing precipitation rates and frequencies) will influence carbon fluxes between carbon pools. In this study we evaluated how the flux (emission) of carbon dioxide (CO_2), a radiatively important gas, is affected by an experimental drought.

The results of the two throughfall reduction experiments that are described in this dissertation have demonstrated that CO_2 emissions from soils under different land uses and different soil conditions can exhibit different sensitivities to drought. While both experiments showed decreases in soil CO_2 production during the respective induced droughts, the effect in the tropical sub-montane rainforest (at the Pono site) was stronger than the effect measured in the cacao / *Gliricidia* agroforestry system. A direct comparison of the drought response mechanisms responsible for the different reactions is difficult considering the contrasting nature of the two ecosystems and the different soil characteristics. We can however conclude that in both ecosystems soil moisture was the primary variable responsible for controlling soil CO_2 production.

In the cacao / *Gliricidia* agroforestry roof experiment, soil CO_2 efflux measurements were only mildly (13 %) suppressed during the course of the 13-month induced drought. These findings corroborate the research findings of Moser *et al.* (2010) and Schwendenmann *et al.* (2010) who studied different physiological reactions in the cacao and *Gliricidia* trees, and likewise concluded that the ecosystem was tolerant to drought stress. These researchers describe how the shallow rooted cacao understory grown next to the deeper rooted *Gliricidia* overstory created a favourable set of site conditions that enabled the ecosystem to mitigate serious drought stress.

We attribute the mild drought response on soil CO_2 efflux to two additional reasons. First, soil CO_2 efflux exhibited an optimal peak at intermediate soil moisture contents but was low when soil conditions became dry (in the induced drought plots), or when the soil became water saturated (in the control plots). This means that respiration differences between control and roof plots may have been masked when soil moisture conditions were saturated in the

control and concurrently were very dry in roof plots. Secondly, soil CO_2 efflux drought response was localized. While at some locations CO_2 efflux decreased in close correlation with soil drying, CO_2 efflux at other measurement sites did not show any drought effects. Overall, the experiment conducted in the cacao / *Gliricidia* agroforestry plantation had a CO_2 neutral effect: emissions were initially reduced during the induced drought but rebounded and surpassed the control during the five month rewetting phase and thus compensated for earlier declines. If in future drought events the severity is similar or less than the drought imposed in our experiment I do not expected a serious risk of carbon imbalances created from sites with this kind of agroforestry system. However, if droughts are severe enough to cause significant tree mortality, effects on the carbon cycle and particular on atmospheric CO_2 feedback potential may be difficult to predict.

In contrast, the sub-montane tropical forest exhibited a strong drought response: soil CO_2 production decreased, tree stem diameter increment decreased (Moser, unpublished data), the understory vegetation experienced severe dieback and tree stem sap flow decreased (Schuldt, unpublished data). A two phase drought response was depicted in the soil CO_2 emission record over the course of induced drought. During the first nine months, CO_2 emissions were only mildly reduced (23 %). This was primarily caused by slowed decomposition of the leaf litter layer. The onset of a natural drought dried the soil to new lows, which subsequently acted as an ecosystem tipping point and triggered drought stress in both root and microbial CO_2 production sources. For the next 15 months CO_2 production decreased (49 %). After the throughfall reduction roof was opened the ecosystem recovery was slow, and CO_2 respiration did not return to normal within the four month rewetting phase. In this ecosystem, soil CO_2 emissions had a positive linear relationship with soil moisture. The fact that overall CO_2 respiration decreased so strongly under the induced drought conditions highlights the sensitivity of this ecosystem to drought and to the carbon cycle.

Although the comparison of the two experiments showed that there were no positive CO_2 emissions released by the soil during the simulated drought (at least during the time period of measurements), it is erroneous to conclude that there were no negative ecosystem interactions with the atmospheric carbon cycle. For instance, drought conditions may also have resulted in physiological carbon allocation changes within trees resulting from decreased photosynthetic carbon uptake. Additionally, vegetation mortality can add significantly to changes in carbon dynamics within the ecosystem.

2   Regional drought effect prediction

At the regional scale, droughts will likely have heterogeneous effects across the landscape, both in natural forests and in cacao agroforests. While some ecosystems will likely exhibit strong signs of drought stress, others will be able to mitigate the impact through either their physiological or morphological traits or because of more favourable micro-site conditions. Biological drought mitigation mechanisms developed by plants to endure drought stresses include: deep and prolific rooting systems which are used to access available water resources; osmotic adjustment to maintain water retention and cell turgor pressure; small and succulent leafs to reduce transpirational water loss; and physiological adaptations to minimize water loss (Farooq *et al.*, 2009). At the biophysical level, site characteristics such as soil type, soil water retention properties and landscape position will also play an important role in determining the extent of the drought impact. Soil CO_2 emissions will accordingly vary depending on the ecosystem drought effect.

Discussions on regional drought response on forest carbon emission dynamics can not exclude the mention of the increased risk of fire in the ecosystem. Burning will not only kill trees but will also volatilize sequestered carbon. Research has shown that during drought events, tropical forests margin especially are at increased risk to slash and burn (Page *et al.*, 2002, Van Nieuwstadt and Sheil, 2005). Where under normal conditions it is difficult to burn a wet tropical forest, natural droughts give farmers the opportunity to clear new farm land.

3   Drought risk prediction in tropical forests

Worldwide, three large-scale *in situ* throughfall displacement experiments have been carried out in tropical forests. In addition to the experiments reported here, two experiments of similar length and design were conducted in the Brazilian Amazon forest, in the: "Caxiuanã National Forest" as reported by Fisher *et al.* (2007) and in "Tapajós National Forest" as reported by Nepstad *et al.* (2002b). In each of the three experiments (including in Pono), droughts effects on soil respiration were measured. The results have been instrumental in illustrating the range of mitigation responses that tropical forest ecosystems can exhibit. The drought response of soil CO_2 production ranged from a severe decrease in soil respiration in Pono, to a moderate effect in Caxiuanã (Sotta *et al.*, 2007), to a very mild effect in Tapajós (Davidson *et al.*, 2004). Since soil respiration and soil CO_2 production is coupled to many ecosystem processes (such as photosynthesis, carbohydrate transfers and microbial activity

(Tang *et al.*, 2005)), I have used it as a general indicator for ecosystem drought stress. A comparison of the experiment sites and drought responses is given in Table 1. Based on the results of the three experiments, which are spread across different soil types and climate zones on different continents, we can begin to speculate why the ecosystems exhibited such contrasting ecosystem responses and soil respiration drought reactions. Although more research is required, it seems that the drought response hinges largely on the range of drought response mechanisms available within an ecosystem. In these three studies we find a close correlation between rooting depth and the intensity of the drought response (in terms of CO_2 production). Likewise, the length of the dry season is correlated positively with rooting depth and negatively with soil CO_2 production drought response.

Table 1:   Comparison of drought response and biophysical site characteristics of three throughfall displacement experiments in tropical forests. The experiment in Caxuianã was conducted by Sotta *et al.* (2007), the experiment in Tapajós was conducted by Davidson *et al.* (2004).

Simulated drought experiment site	Length of the experiment (months)	Drought effect on soil CO_2 efflux (compared to control plot emissions)	Dry season length in months (<60 mm)	Mean annual precipitation (mm)	Maximum rooting depth of coarse roots (m)	Soil texture class
Pono, Sulawesi, Indonesia	31	- 39 %	0	2,901 *	< 0.8	Clay loam
Caxuianã, Brazil	23	- 22 %	1	2,272	< 5	Sandy loam
Tapajós, Brazil	51	+ 18 %	3	2,000	>10	Clay

* Data from 2008

It is generally accepted that ecosystems adapt to their local biophysical environment. Accordingly, tropical forest ecosystems may or may not have developed appropriate drought response mechanisms depending on the historic climatic conditions of the area. At sites like Tapajós in Brazil for example, where there is a pronounced annual dry period, ecosystems have adapted appropriate mechanisms, including deeper rooting architectures to access deep water resources. In contrast, regions where historically there are no pronounced dry seasons, such as in central Sulawesi, ecosystems have not needed to develop appropriate drought mitigation strategies. A review paper by Schenk and Jackson (2002), supported the observation that rooting depth increases with increasing dry season length. Inversely, rooting depth decreased with increased overall precipitation.

If we assume that the length of the dry season is a good indicator of drought adaptation we might be able to extrapolate ecosystem drought risks simply by using this parameter (length of dry season) alone. Using the WORLDCLIM monthly precipitation dataset (1-km spatial resolution) (Hijmans *et al.*, 2005), I calculated the number of consecutive dry months (less than 60mm per month) across the tropics (Fig. 1). The derived map highlights regions that are potentially vulnerable to droughts, should they occur. Areas on the map having a short dry season are less adapted to drought, while areas with long dry seasons have adapted appropriate drought response mechanisms. Accordingly and with caution, given that there are only three such drought experiments conducted, we could extrapolate CO_2 production drought responses to the tropics: whereby the Pono case study might represent possible dynamics exhibited by forests at high risk, and the Tapajós drought forests at low risk.

It should be recognized however that there are some limitations to this drought risk map. First, the lack of a dry season does not automatically mean that the ecosystem is vulnerable to drought. For instance, ecosystems may have developed drought adaptations by the periodic exposure to natural drought events which do not occur seasonally. Second, ecosystem adaptations to the climate require very long time periods (centuries or longer) to realize in nature. The WORLDCLIM climate dataset on the other hand, used here has averaged climate patterns from the last few decades and therefore may not accurately reflect actual climate – ecosystem adaptations. Third, since the WORLDCLIM dataset is calculated using an interpolation algorithm between climate stations, regions where there are few climate stations (such as in the heart of the Amazon forest) estimates may not be completely accurate. Lastly, the map does not consider site characteristics, such as soil water holding capacities from different textured soils or landscape position. Despite the uncertainties, the map represents initial steps towards extrapolating results achieved from these three cross-continental tropical forest drought experiments into a biome wide context.

The research presented in this thesis provides new insights in the complex nature of tropical ecosystem dynamics in responses to a changing climate. The findings contribute to the topical discussion on drought effects on forest-atmospheric biogeochemical interactions and also on belowground CO_2 production dynamics in tropical forest environments of SE Asia.
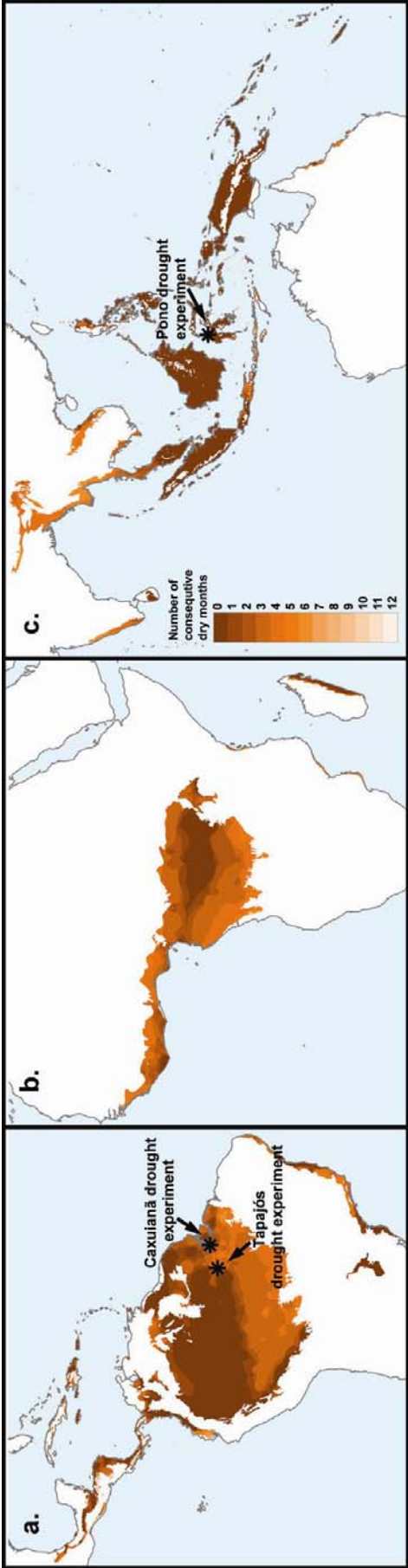
Figure 1: Potential drought risk map for natural tropical forests, using the number of consecutive dry months as a proxy for drought sensitivity, in (a) Latin America, (b) Africa and (c) Asia

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DECLARATION OF ORIGINALITY AND CERTIFICATE OF OWNERSHIP

I, Oliver van Straaten, hereby declare that I am the sole author of this dissertation entitled "Drought effects on soil carbon dioxide efflux in two ecosystems in Central Sulawesi, Indonesia". All references and data sources that were used in the dissertation have been appropriately acknowledged. I furthermore declare that this work has not been submitted elsewhere in any form as part of another dissertation procedure.

Goettingen, February 19, 2010   _____

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